

2009

## The role of climate variability and riverine pulsing in the community dynamics of estuarine nekton in Breton Sound, Louisiana

Bryan Patrick Piazza

*Louisiana State University and Agricultural and Mechanical College*

Follow this and additional works at: [https://digitalcommons.lsu.edu/gradschool\\_dissertations](https://digitalcommons.lsu.edu/gradschool_dissertations)



Part of the [Oceanography and Atmospheric Sciences and Meteorology Commons](#)

---

### Recommended Citation

Piazza, Bryan Patrick, "The role of climate variability and riverine pulsing in the community dynamics of estuarine nekton in Breton Sound, Louisiana" (2009). *LSU Doctoral Dissertations*. 2974.

[https://digitalcommons.lsu.edu/gradschool\\_dissertations/2974](https://digitalcommons.lsu.edu/gradschool_dissertations/2974)

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Doctoral Dissertations by an authorized graduate school editor of LSU Digital Commons. For more information, please contact [gradetd@lsu.edu](mailto:gradetd@lsu.edu).

THE ROLE OF CLIMATE VARIABILITY AND RIVERINE PULSING IN THE  
COMMUNITY DYNAMICS OF ESTUARINE NEKTON IN BRETON SOUND, LOUISIANA

A Dissertation

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by

Bryan Patrick Piazza

B.S., University of Wisconsin-Stevens Point, 1993

M.S., Louisiana State University, 1997

May 2009

## **ACKNOWLEDGEMENTS**

It took a village to raise this researcher, and now I would like to thank my village. First off, I would like to thank my advisor, Megan La Peyre. I have enjoyed working and learning with you, immensely. Your perspective and viewpoints have consistently led to intellectual growth, personal discovery, and self-improvement. I hope to continue working together for a long time. I also appreciate the efforts of my committee: Kenny Rose, Jaye Cable, Barry Keim, Lawrence Rozas, and Harris Wong. Your efforts, previous research, and willingness to talk about ideas have made me better.

None of this research could have been accomplished without funding. This body of work was funded by the Louisiana Governor's Applied Coastal Research and Development Program (LACRDP), the Coastal Restoration and Enhancement through Science and Technology (CREST) Program, Louisiana Department of Wildlife and Fisheries, the Louisiana Sea Grant College Program, and the USGS Cooperative Research Unit program.

I also received funding and support for a trip abroad to participate as a visiting scientist at Fudan University in Shanghai, China and present my research at the World Fisheries Congress in Yokohama, Japan. This experience was an integral component of my Ph.D. experience. It broadened my intellectual horizon, honed my communication skills, and expanded my professional network greatly. Thanks to Lawrence Rozas for introducing me to the researchers at the Institute of Biodiversity Science at Fudan University and Kenny Rose for providing advice and contacts in Yokohama. Thank you also to the School of Renewable Resources, Department of Oceanography and Coastal Sciences, School of the Coast and Environment (LSU), the American Fisheries Society, and Sigma Xi Scientific Research Society (LSU Chapter) for funding support.

I also appreciate the efforts of everyone who helped me in the field and lab: Chris Cannaday, Wes Cochran, Whitney Gayle, Bryan Gossman, Chris Llewellyn, Sarai Piazza, Adam Piehler, Mason Piehler, Sergio Pierliuissi, and Aaron Podey. I would especially like to thank Shawn Hillen (JHT), the master of drop sampling, for taking care of the boat and drop sampling equipment so that I could concentrate on the other essentials of the job. I greatly respect his knowledge and die-hard work ethic. He is a model for anyone who wants to develop mastery over the art of field work. The Baltz lab provided me with a drop sampling boat and equipment when I needed it. Deb Kelly, Jerome La Peyre and Naoki Itoh provided laboratory access, assistance, direction, and extreme patience while I was navigating the new world of nucleic acid purification and quantification. Cromwell Espineda (Qiagen, Inc.) provided technical assistance with the Qiagen AllPrep DNA/RNA Mini Kit, and without his help and patience, my growth experiments would not have been possible. A special thanks to Derek King for all his hard work while we navigated through nucleic acid purification and measurement. Derek stuck with me from beginning to end, and I could not have done my growth study without him. Jim Cowan and Andy Fischer provided access to and instruction on the bomb calorimeter.

My work in Breton Sound could not have been accomplished without the help of several agencies and resource managers. Chuck Villarubia and Tom Bernhard (Louisiana Department of Natural Resources, Coastal Restoration Division) and the Caernarvon Interagency Advisory Committee provided experimental riverine pulses. Lonnie Serpas (Plaquemines Parish) operated the Caernarvon diversion and was always just a cell phone call away if we got in a bind while in the field. The USGS National Wetlands Research Center provided a trailer for lodging after Hurricane Katrina, when not much else was standing in the area. Louisiana Department of Wildlife and Fisheries, Marine Fisheries section collected the long-term fisheries independent

and environmental data. Michael Beck (Louisiana Department of Natural Resources, Coastal Restoration Division) cleaned and provided the original long-term data sets, and then worked with me to ensure the integrity of the data. Kyle Brehe (Southern Regional Climate Center) provided me with weather data. Gregg Snedden (USGS) provided input and assistance with time series data analysis. Michelle Fischer (USGS) created and edited study area maps. A special thanks to Delacroix Corporation, especially Mike Benge and Michael Farizo for providing land access rights, lodging, and support of LSU coastal research. Whether it was providing lodging at their wonderful camp in the marsh, bringing diesel fuel for the generator, or helping me to keep my research going after Hurricane Katrina, even when they were dealing with great personal loss. I took great comfort in knowing that help was only a phone call away.

Thank you to those who provided thoughtful reviews of my manuscripts: Tom Minello (NOAA Fisheries Service), Sarai Piazza, Greg Steyer, Kari Cretini, and Gregg Snedden (USGS), Brian Roth and Guerry Holm, and Barry Keim (LSU), and Joel Trexler (FIU).

On a personal note, I would like to thank my friends (especially the inner sanctum...you know who you are) for always giving me a laugh and a beer when I was geeking out too hard. Thank you to my mom, Patricia Piazza, for teaching me to read, sacrificing to give me a great education, and nurturing and supporting my deep desire and talent for learning. I would like to thank my wife, Sarai, for working hard with me. You are my rock and the consummate partner. I pick you first for my team every time. Lastly, to my new son, Kade, your gestation was a great inspiration. I hope that my work will make your life better and ensure that you and yours have as many good times in the marsh as I have had.

## TABLE OF CONTENTS

ACKNOWLEDGEMENTS .....	ii
LIST OF TABLES .....	ix
LIST OF FIGURES .....	xi
ABSTRACT .....	xv
CHAPTER 1. GENERAL INTRODUCTION .....	1
BACKGROUND .....	1
RESEARCH OBJECTIVE .....	5
STUDY AREA .....	6
SYNOPSIS OF CHAPTERS .....	6
LITERATURE CITED .....	8
CHAPTER 2. RELATING LARGE-SCALE CLIMATE VARIABILITY TO LOCAL SPECIES ABUNDANCE: ENSO FORCING AND BROWN SHRIMP ( <i>FARFANTEPENAEUS</i> <i>AZTECUS</i> ) IN BRETON SOUND, LOUISIANA, USA.....	11
INTRODUCTION .....	11
Study Area .....	14
METHODS .....	16
Data Sources .....	16
Brown Shrimp Abundance Data .....	16
Environmental Data .....	17
Climate and Meteorological Data .....	18
Remote Wind Forcing.....	19
Mississippi River Discharge .....	19
Yearly Anomaly Calculations.....	20
Statistical Analyses .....	21
RESULTS .....	22
ENSO .....	22
ENSO and Weather.....	23
ENSO and Environmental Conditions.....	27
ENSO and Juvenile Brown Shrimp Abundance .....	28
ENSO-Forced Environmental Assembly Filters.....	28
DISCUSSION.....	30
ENSO and Weather.....	31
ENSO and Brown Shrimp.....	31
ENSO-Forced Environmental Assembly Filters.....	32
Neutral ENSO Years.....	35
Management Implications.....	36
LITERATURE CITED .....	37

CHAPTER 3. RESTORATION OF THE ANNUAL FLOOD PULSE IN BRETON SOUND, LOUISIANA, USA: HABITAT CHANGE AND NEKTON COMMUNITY RESPONSE .....	42
INTRODUCTION .....	42
MATERIALS AND METHODS .....	44
Study Area .....	44
Site Selection .....	45
Nekton and Environmental Data Collection .....	46
Data Analysis .....	48
Environmental Variables .....	48
Nekton Density, Biomass, Diversity .....	48
Nekton Communities .....	48
RESULTS .....	50
Environmental Variables .....	50
Nekton Density, Biomass, and Diversity .....	50
Nekton Community Assembly .....	55
C-score Analysis .....	55
Canonical Correspondence Analysis .....	56
DISCUSSION .....	56
Water Depth and Flooding Duration .....	59
Nekton Densities .....	60
Nekton Diversity and Community Assembly .....	62
LITERATURE CITED .....	65

CHAPTER 4. USING <i>GAMBUSIA AFFINIS</i> GROWTH RATES TO ASSESS ESTUARINE HABITAT QUALITY: A COMPARISON OF INDICES .....	69
INTRODUCTION .....	69
Study Area .....	72
METHODS .....	74
Laboratory Experiment 1: Precision of Nucleic Acid Purification Technique .....	74
Experimental Design .....	74
Data Analysis .....	74
Laboratory Experiment 2: Growth Experiment .....	74
Experimental Setup and Design .....	75
Data Analysis .....	76
Field Experiment 1: Enclosure Growth Experiment .....	77
Experimental Setup and Design .....	77
Data Analysis .....	77
Field Experiment 2: Through-Pulse Field Collection Experiment .....	78
Experimental Design .....	78
Data Analysis .....	79
Experimental Protocols .....	79
Nucleic Acid Indices .....	79
Length-Weight Condition .....	80
Energy Density .....	81
RESULTS .....	81
Laboratory Experiment 1: Precision of Nucleic Acid Purification Technique .....	81

Laboratory Experiment 2: Growth Experiment .....	81
Fish Recovery .....	81
Fish Growth .....	81
Nucleic Acid Indices:.....	82
Length-Weight Condition .....	82
Comparison of Techniques .....	82
Field Experiment 1: Enclosure Growth Experiment.....	83
Environmental Characteristics .....	83
Fish Recovery .....	84
Fish Growth .....	84
Nucleic Acid Indices.....	86
Length-Weight Condition .....	86
Comparison of Techniques .....	86
Field Experiment 2: Through-Pulse Field Collection Experiment .....	86
Environmental Characteristics .....	86
Fish Growth .....	87
Nucleic Acid Indices.....	88
Length-Weight Condition .....	88
Energy Density.....	88
Comparison of Techniques .....	90
DISCUSSION .....	92
Growth and Habitat Quality.....	94
Growth Indices.....	96
Conclusions.....	98
LITERATURE CITED .....	99
 CHAPTER 5. THE EFFECT OF HURRICANE KATRINA ON NEKTON COMMUNITIES IN THE TIDAL FRESHWATER MARSHES OF BRETON SOUND LOUISIANA, USA.....	103
INTRODUCTION .....	103
Study Area .....	104
METHODS .....	108
Data Analysis .....	109
Environmental Conditions .....	109
Nekton Density, Biomass, Diversity.....	109
Nekton Communities .....	110
RESULTS .....	110
Environmental Characteristics.....	110
Nekton Density, Biomass, Diversity, and Communities .....	111
DISCUSSION .....	117
Nekton Community Change .....	117
Nekton Community Recovery and Ecosystem Resilience.....	119
CONCLUSION.....	121
LITERATURE CITED .....	122
 CHAPTER 6. SUMMARY AND CONCLUSIONS .....	125



APPENDIX A. CHAPTER 2 SUPPLEMENTAL GRAPHS.....	130
APPENDIX B. LETTER REQUESTING REPRINT PERMISSION.....	135
VITA.....	139

## LIST OF TABLES

Table 2.1. Classification of ENSO events in the winter season (January – March) for the period of record (1988 – 2007) and based on a five month running mean of the Niño 3.4 sea surface temperature anomaly index. Value in parentheses is running mean SSTA value...	24
Table 2.2. Pearson ( <i>r</i> ) correlations between Niño 3.4 sea surface temperature anomaly (SSTA) index (lagged 0 – 12 months), brown shrimp ( <i>Farfantepenaeus aztecus</i> ) abundance, and environmental conditions in Breton Sound, Louisiana, USA. Data for SSTA, brown shrimp abundance, salinity, and water temperature are based on N = 240 monthly means. Data for water level is based on N = 192 monthly means. Values in bold are significant at $\alpha = 0.05$ .	25
Table 2.3. Monthly mean $\pm$ SE (range) values of spring (April – June) salinity and water temperature variables as measured at four fisheries independent seine net collection stations (244, 255, 250, 251) in Breton Sound estuary, Louisiana during the period of record (1988 – 2007).	27
Table 3.1. Number of days and sites sampled during both (February 14 to 28, March 12 to 28) Caernarvon experimental high-flow pulse events in 2005. Nekton sampling in both inflow and reference areas was restricted to days that the marsh surface was flooded. Maximum structure discharge during both pulse events was $184 \text{ m}^3 \text{ s}^{-1}$ .	46
Table 3.2. Environmental characteristics of samples in inflow and reference areas during Caernarvon experimental high-pulse flows in 2005. Data for inflow and reference areas are mean $\pm$ SE (range). Effects — P: pulse; T: treatment. * $p < 0.05$ ; ** $p < 0.01$ ; *** $p < 0.001$ .	52
Table 3.3. Mean nekton density (ind. $\text{m}^{-2}$ ) by species during the February and March 2005 Caernarvon experimental high-pulse flow events in Breton Sound, Louisiana, USA. Data are mean $\pm$ SE. Gray shading indicates the species of highest density by pulse and treatment.	54
Table 4.1. Commonly used morphometric and biochemical growth indices for fish and key review papers.	70
Table 4.2. Lab experiment 2: Growth experiment. Summary statistics by treatment for cellular RNA and DNA concentrations and nucleic acid growth indices. Nucleic acids were purified from wild <i>Gambusia affinis</i> caught in upper Breton Sound, Louisiana during summer 2007 and used in the 10-day laboratory feeding experiment. Means are based on N = 207 tank means.	83
Table 4.3. Lab experiment 2: Growth experiment. Pearson product moment correlation results for nucleic acid-based growth indices and somatic daily growth during a 10-day laboratory experiment with wild <i>Gambusia affinis</i> . All correlations are based on N = 207 daily tank means. Fish weight and total length were significantly correlated; therefore only	

correlations with weight are reported. P-values are located within parentheses, and bold type signifies statistical significance at $\alpha = 0.05$ . .....	84
Table 4.4. Field experiment 1 and 2: Environmental characteristics of upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. The enclosure experiment, began at week six of the pulse and lasted 10 days. The field collection experiment began on the first day of the pulse event and lasted seven weeks.....	87
Table 4.5. Field experiment 1: Enclosure experiment. Summary statistics by treatment for morphometric and nucleic acid growth indices for wild <i>Gambusia affinis</i> during a short-term enclosure growth experiment in upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. The enclosure experiment, began at week six of the pulse and lasted 10 days. The rate of change in TL is reported, as opposed to SL, in order to remain consistent across experiments. The change in SL was also measured and the results are the same as TL.....	90
Table 4.6. Field experiment 2: Through-pulse field collection. Summary statistics by treatment for nucleic acid growth indices for wild <i>Gambusia affinis</i> during a through-pulse field collection experiment in upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. The field collection experiment began on the first day of the pulse event and lasted seven weeks. ....	91
Table 4.7. Field experiment 2: Through-pulse field collection. Pearson product moment correlation results for nucleic acid-based growth indices and mean weight (g DW) of wild-caught <i>Gambusia affinis</i> in upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. Field collections began on the first day of the pulse event and lasted seven weeks. Correlations for all indices except energy density are based on N = 208 fish. Comparisons with energy density are based on N = 36 one-gram DW pellets, composed of 1,828 fish. Fish weight and total length were significantly correlated; therefore only correlations with weight are reported. P-values are located within parentheses, and bold type signifies statistical significance at $\alpha = 0.05$ . .....	92
Table 5.1. Mean ( $\pm$ SE) and range of environmental characteristics (water temperature, salinity, dissolved oxygen, turbidity, vegetative cover, water depth) measured on the flooded marsh surface in upper Breton Sound estuary, Louisiana during nekton sampling in spring 2005 – 2007 through winter-spring riverine pulse events. ....	113
Table 5.2. Mean nekton density (ind. m <sup>-2</sup> ) and percent occurrence in drop samples by species pre- (2005) and post-Hurricane Katrina (2006, 2007). Nekton were sampled on the flooded marsh surface in upper Breton Sound estuary, Louisiana during winter-spring riverine pulse events in spring 2005-2007. Residence status classification is as follows: T/R = Tidal Freshwater/Resident; B/M = Brackish/Migrant. Definitions for both categories are given in the text.....	115

## LIST OF FIGURES

Fig. 1.1. Conceptual model showing how climate controls local estuarine nekton community structure. Items in black were addressed in this dissertation. ....	4
Fig. 2.1. Map of Breton Sound estuary, Louisiana, USA. Dots mark the location of four fisheries independent seine net collection stations used in this study. Triangle marks the location of USGS 07374527 Northeast Bay Gardene near Point-a-la-Hache, LA. Square marks the location of New Orleans International Airport (Sta. Id. 166295). ....	15
Fig. 2.2. Graph of the five month running mean of the Niño 3.4 sea surface temperature anomaly index. Dashed lines border the neutral classification area. Values above the upper dashed line correspond to El Niño months, and values below the lower dashed line correspond to La Niña months. ....	23
Fig. 2.3. Mean (SE) winter (January – March), (A) surface atmospheric pressure, (B) precipitation, (C) air temperature, (D) Mississippi River discharge, (E) wind forcing, and (F) water level anomalies by ENSO classification. Air pressure, precipitation, air temperature, and wind forcing variables were measured at New Orleans International Airport (Sta. Id. 166295). Mississippi River discharge was measured at Tarbert’s Landing, Mississippi (Gage Id. USACE 01100). Water level was measured at USGS 07374527 Northeast Bay Gardene near Point-a-la-Hache, LA. Anomalies for A – E are based on the period of record, 1988 – 2007, and anomalies for F are based on the period of record 1992 – 2007. ....	26
Fig. 2.4. Mean (SE) spring (April – June), (A) brown shrimp, (B) salinity, and (C) water temperature anomalies by ENSO classification, based on the period of record (1988 – 2007). Brown shrimp abundance, salinity, and water temperature variables were measured at four fisheries independent seine net collection stations (244, 255, 250, 251) in Breton Sound estuary, Louisiana. Mean brown shrimp anomalies are based on normalized abundance data. ....	29
Fig. 2.5. Mean (SE) monthly shrimp catch in seine samples in Breton Sound estuary, Louisiana, USA from 1988 – 2007. Means are based on a combined mean from four fisheries independent seine net collection stations (244, 255, 250, 251). ....	30
Fig. 3.1. Breton Sound estuary, Louisiana, USA and the location of the Caernarvon Freshwater Diversion. Shaded areas show the locations of the inflow (light gray) and reference (dark gray) areas used in this study. Map is adapted from Snedden et al. (2007b). ....	45
Fig. 3.2. Hydrograph showing water and marsh level before and during both experimental high-pulse flow events in 2005. Pulses dates were February 14–28 and March 12–28. Feb-I: February pulse inflow area; Feb-R: February pulse reference area; Mar-I: March pulse inflow area; Mar-R: March pulse reference area. Source datum for stages and water level in the inflow area was the National Geodetic Vertical Datum, NGVD. Because there was no surveyed water level recorder in the reference area, stages and marsh level were based on an investigator-created datum, transferred from USGS 073745257. ....	51

- Fig. 3.3. (A) Water depth (cm), (B) nekton density (ind m<sup>-2</sup>), and (C) Shannon-Wiener Diversity (H') at flooded marsh sampling sites during the Caernarvon experimental high-pulse flow events in 2005 (data are mean  $\pm$  SE). Samples — black; reference; grey; inflow. Letters denote significant statistical differences within and between pulse events. Mean biomass (g m<sup>-2</sup>) and mean Shannon-Wiener Evenness, E (both measures not shown) followed the same pattern as density, and, diversity, respectively. .... 53
- Fig. 3.4. Species rank curves for nekton assemblages caught at flooded marsh sampling sites during the Caernarvon experimental high-pulse flow events in 2005. Samples — black; inflow; grey; reference. Nekton abundance for inflow samples was an order of magnitude higher than the y-axis. .... 55
- Fig. 3.5. Association of environmental variables and nekton species based on canonical correspondence analysis for all sites in Breton Sound estuary through 2 (February and March) high-flow pulse events of the Caernarvon Freshwater Diversion structure in 2005. Displayed environmental variables are statistically significant at  $\alpha=0.05$ . Bold: dominant species (see Table 3 for full names). .... 57
- Fig. 3.6. Top 6 nekton species abundances as a function of water depth during Caernarvon experimental pulse events. Samples from all sites (inflow and reference) and pulse events (February and March) were combined. .... 58
- Fig. 4.1. Map showing Breton Sound estuary, Louisiana and the location of the Caernarvon Freshwater Diversion. Shaded areas show the location of the inflow (light gray) and reference (dark gray) areas used in this study. Map taken from Piazza & La Peyre (2007). .... 73
- Fig. 4.2. Lab experiment 2: Growth experiment. Comparison of (A) daily mean weight (g DW), (B) RNA:DNA, and (C) length-weight condition for wild-caught *Gambusia affinis* through a 10-day laboratory growth experiment. Fish in the fed treatment were fed a commercial flake food *ad-libitum* every six hours for 10 days. Fish in the starved treatment were withheld food during the 10 day period. Comparisons of growth rate and RNA:DNA are based on N = 207 tank means. Length-weight condition is based on N = 610 fish. In all graphs, black represents fed fish, and gray represents starved fish. .... 85
- Fig. 4.3. Field experiment 1: Enclosure growth. Comparison of (A) daily growth (g DW d<sup>-1</sup>) index, (B) RNA:DNA, and (C) length-weight condition for wild-caught *Gambusia affinis* through a 10-day field enclosure growth experiment in upper Breton Sound, Louisiana. Inflow fish were contained in enclosures in flooded marsh habitat for 10 days beginning at week six of an extended freshwater pulse event downstream from the Caernarvon Freshwater Diversion. Reference fish were contained in flooded marsh habitat unaffected by the freshwater pulse. Comparisons of growth rate, RNA:DNA, and length-weight condition are based on N = 37 experimental fish (26 inflow, 11 reference) recaptured in enclosures after the 10-day experiment. In all graphs, black represents inflow fish, and gray represents reference fish. .... 89
- Fig. 4.4. Field experiment 2: Through-pulse field collection. Comparison of (A) weekly mean weight (g DW) and (B) RNA:DNA indices, as well as (C) weekly energy density (cal g<sup>-1</sup>)

and (D) length-weight condition for wild-caught *Gambusia affinis* through a seven week freshwater pulse event in upper Breton Sound, Louisiana. Inflow fish were captured weekly in flooded marsh habitat downstream from the Caernarvon Freshwater Diversion beginning on the first day of the pulse event. Reference fish were captured weekly in flooded marsh habitat unaffected by the freshwater pulse. Comparisons of growth rate and RNA:DNA are based on N = 208 fish (104 inflow, 104 reference), and comparisons of energy density and length-weight condition are based on N = 1,828 fish. In all graphs, black represents inflow fish, and gray represents reference fish..... 93

Fig. 5.1. Maps showing Breton Sound estuary, Louisiana and (A) wind speed ( $\text{km h}^{-1}$ ) and (B) storm surge height (m) during Hurricane Katrina. The white stippled area in both maps delineates the boundary of the tidal freshwater marshes where nekton were sampled during this study. The storm track of Hurricane Katrina is shown as a dashed black and white line on both the maps and inset. The square on panel B indicates the position of the United States Geological Survey (USGS) National Water Information System station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253). Wind speed data are from NOAA, Atlantic Oceanographic and Meteorological Laboratory ([http://www.aoml.noaa.gov/hrd/Storm\\_pages/katrina2005/wind.html](http://www.aoml.noaa.gov/hrd/Storm_pages/katrina2005/wind.html)). Water level contours are based on an ADCIRC coastal storm surge model and are modified from US Army Corps of Engineers (2006; <https://ipet.wes.army.mil>) and Keim and Muller (In Press). Water level points (white dots) are observed high water marks from the Federal Emergency Management Agency (FEMA 2006, map B-12). Background image (Landsat Thematic Mapper 5) is from October 28, 2006. .... 105

Fig. 5.2. Photographs showing the physical habitat change due to Hurricane Katrina. The first set of photographs (A,B) illustrate the large scale vegetated marsh loss that occurred in Breton Sound estuary as a result of Hurricane Katrina. The area inside the red oval in Fig 2A is the area in Fig 2B. Also shown is a small-scale illustration of the pre- (C) and post-hurricane (D) condition of the marshes sampled during this study. Photos A and B are taken from Barras (2007), and photos C and D are courtesy of S. Piazza, U.S. Geological Survey, National Wetlands Research Center, Coastal Restoration Field Station, Baton Rouge, LA. .... 108

Fig. 5.3. Hydrographs of continuous A) water level and B) salinity from January 1, 2005 – December 31, 2007, taken at United States Geological Survey (USGS) National Water Information System station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253). The vertical dashed line marks the passage of Hurricane Katrina. .... 112

Fig. 5.4. Mean ( $\pm$  SE) A) nekton density ( $\text{ind. m}^{-2}$ ), and B) Shannon-Weiner Diversity ( $H'$ ), of nekton caught at flooded marsh sampling sites pre- (spring 2005) and post-Hurricane Katrina (spring 2006, 2007). Capital letters denote significant statistical differences ( $\alpha = 0.05$ ) between years. Graph C shows the percentage of total nekton abundance that belonged to either the Tidal Freshwater/Resident group (T/R; black) or the Brackish/Migrant group (B/M; gray) for the same years. Species were grouped according to salinity tolerance and life-history characteristics, and definitions are provided in the text. .... 114

Fig. A.1. Graph of salinity in Breton Sound estuary, Louisiana from 1988 – 2007. Time series is based on monthly means of discrete samples pooled across stations 244, 255, 250, and 251.....	130
Fig. A.2. Graph of water temperature (° C) in Breton Sound estuary, Louisiana from 1988 – 2007. Time series is based on monthly means of discrete samples pooled across stations 244, 255, 250, and 251.....	130
Fig. A.3. Graph of air temperature (° C) taken at the New Orleans International Airport (Sta. Id. 166295) from 1988 – 2007. Time series is based on monthly means of continuous hourly readings.....	131
Fig. A.4. Graph of air pressure (mb) taken at the New Orleans International Airport (Sta. Id. 166295) from 1988 – 2007. Time series is based on monthly means of continuous hourly readings.....	131
Fig. A.5. Graph of precipitation (cm) taken at the New Orleans International Airport (Sta. Id. 166295) from 1988 – 2007. Time series is based on monthly means of continuous hourly readings.....	132
Fig. A.6. Graph of normalized juvenile brown shrimp abundance in Breton Sound estuary, Louisiana from 1988 – 2007. Time series is based on monthly means of discrete seine samples normalized by the mean and standard deviation and pooled across stations 244, 255, 250, and 251.....	132
Fig. A.7. Graph of the monthly Nino 3.4 SSTA index and monthly salinity in Breton Sound estuary, Louisiana. Graph is based on the six-month running mean of the Nino 3.4 SSTA and monthly mean salinity from discrete samples pooled across stations 244, 255, 250, and 251.....	133
Fig. A.8. Graph of the monthly salinity and juvenile brown shrimp abundance in Breton Sound estuary, Louisiana. Salinity values are monthly means pooled across stations 244, 255, 250, and 251. Brown shrimp abundance values are monthly means of normalized values (normalized by the mean and standard deviation) pooled across stations 244, 255, 250, and 251.....	133
Fig. A.9. Graph of the monthly state of the ENSO and monthly juvenile brown shrimp abundance in Breton Sound estuary, Louisiana. ENSO values are the six-month running mean of the Niño 3.4 SSTA index. Brown shrimp abundance values are monthly means of normalized values (normalized by the mean and standard deviation) pooled across stations 244, 255, 250, and 251.....	134

## ABSTRACT

Climate controls biotic community composition at multiple spatiotemporal scales through variability in environmental control mechanisms (assembly filters). This research investigated the role of climate variability in the community dynamics of estuarine nekton in Breton Sound estuary, Louisiana, and, specifically the effects of El Niño Southern Oscillation (ENSO), freshwater discharge, and a tropical cyclone. A teleconnection was found between ENSO and juvenile brown shrimp (*Farfantepenaeus aztecus*) abundance in Breton Sound from 1988 – 2007. ENSO affected winter weather conditions (air pressure, temperature and precipitation), and spring brown shrimp abundance in Breton Sound. Juvenile brown shrimp abundance lagged ENSO by three months; below-average abundance of juvenile brown shrimp was caught in springs following El Niño winters while above-average abundance of brown shrimp was caught in springs following La Niña winters. Salinity was the dominant ENSO-forced assembly filter that regulated brown shrimp abundance. Study of short-term freshwater pulses revealed higher nekton density and biomass in marshes receiving pulsed riverine flow (inflow) than in reference marshes, due to differences in water depth and flooding duration caused by the pulses. Communities consisted mainly of marsh resident species; individual-species examination revealed habitat preference related to water depth. Inflow marshes were capable of producing optimum growth of *Gambusia affinis* ( $0.001 \text{ g DW d}^{-1}$ ) and energetically valuable habitat ( $> 6,000 \text{ cal g}^{-1}$ ) for trophic transport. Riverine pulses may enhance secondary productivity in Breton Sound estuary. Breton Sound was directly hit by Hurricane Katrina in 2005, causing extreme physical habitat damage and a protracted period of elevated salinity in tidal freshwater marshes. Results included higher nekton densities and a nekton community shift from one dominated by Tidal freshwater / Resident (T/R) species toward one that included Brackish / Migrant species. Effects were short lived; by spring 2007, the nekton community had returned to



T/R species, despite the lasting loss of vegetated marsh habitat. These findings provide greater understanding of large-scale climate effects on local estuarine nekton community dynamics and productivity.

# **CHAPTER 1**

## **GENERAL INTRODUCTION**

### **BACKGROUND**

Climate is the ultimate source of environmental variability. It is the result of a complex system consisting of astronomic, atmospheric, terrestrial, oceanic, and ice systems that function to distribute energy around the globe (Oliver & Hidore 2002). Climatic variability is expressed in atmospheric circulation systems and corresponding weather patterns that occur on many time scales and affect many spatial scales. Variation may last from days (frontal passage) to weeks (wet periods, cold snaps), months (teleconnection patterns), years (warm decade, several cold winters), and centuries (glacials, interglacials). Areas affected range in size from local habitats to continents and often are the result of processes that occur large distances away and involve the coupling of atmospheric and oceanic processes (e.g. El Niño Southern Oscillation; hereafter ENSO). The end result of this climatic expression is physical disturbance to habitats.

Climate-induced disturbance has long been understood as the ultimate controlling factor for biotic populations and species diversity. Darwin (1859) wrote, “Climate plays an important part in determining the average numbers of a species and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks.” (p. 54). Clements (1916) named climate as both the ultimate determinant of climax vegetative communities and the cause of the random disturbance that retards succession. In more recent times, several theories have emerged to explain links between climate and disturbance. The Theory of Climatic Stability (Klopfer 1959, Pianka 1966) asserted that the species diversity attained in the tropics was due to stable climate, which corresponds to finer niche specialization and smaller species space requirements. Connell (1978) theorized that climate-induced physical disturbances, intermediate in frequency

and intensity, produce the greatest species diversity by keeping systems in non-equilibrium. The Pulsing Paradigm (Odum et al. 1995) redefined non-equilibrium by stating that ecological systems are constantly pulsing, both physically and biologically, thereby keeping them in a state of “pulsing equilibrium,” and consequently, the greatest energy is realized in ecosystems when resonance occurs between physical and biological pulses. While these theories differ in details, they all suggest mechanisms of climatic control of species assemblage at the local level. Community assembly theory defines climate-induced environmental control mechanisms as assembly filters.

Climate-induced assembly filters ultimately determine biotic community composition at multiple spatial and temporal scales (Tonn 1990, Keddy 1999, Weiher & Keddy 1999). While evolution determines the ultimate size and composition of the species pool, biota at the largest temporal and spatial scales are influenced by large-scale forcing (geophysical events) and long-term climate factors (Williams et al. 2003). As such, biota must pass through a series of environmentally-derived filters, such that the regional species pool is a subset of the continental species pool, and the local species pool is a subset of the regional species pool (Tonn 1990). Tonn studied fish community structure in small northern-temperate freshwater lakes in the United States, Canada, and Finland and identified climate-induced filters in these systems at multiple scales, down to the local level. He argued the necessity of identifying local community response to climate-induced forcing and advocated the extension of his conceptual process to other aquatic systems.

Estuaries are physically dominated habitats where their abiotic forcing attributes (i.e. water flow) are readily apparent (Day et al. 1989). Atmospheric processes dictate the contribution of fluvial and marine influence, water flow variability, and, ultimately, local estuarine dynamics (Fig. 1.1). Climate-induced variability in these abiotic forcing mechanisms

affects estuarine hydroperiod, salinity, sedimentation, and nutrient dynamics, all potential community assembly filters for estuarine flora and fauna.

Life histories of estuarine fauna are intimately tied to water flow pulsing. Many larval-stage estuarine transient species are recruited into the estuary by advective processes that carry them from the coastal ocean, and variability in atmosphere-ocean processes affect ocean currents, thus encouraging or retarding recruitment of certain species (Turner & Brody 1983, Epifano 1995, Brown et al. 2000, Bradbury & Snelgrove 2001). For example, Hofmann & Powell (1998) showed that slowing and strengthening of warm-water gulf-stream eddies off Cape Hatteras decreased larval fish survival and recruitment to shelf waters. Davis (2000) found assemblage differences in three tidepool fish in California during El Niño and La Niña events and linked them to changes in recruitment from advective currents. Resident species (i.e. *Crassostrea virginica*) are also transported within the estuary by circulation patterns that distribute their planktonic larvae, and water flow variation often dictates the spatial distribution of those larvae (Cake 1983, Hofmann & Powell 1998). Resident nekton species (i.e. Poeciliidae) are also linked to climatically-driven flood events for reproduction, survival, and growth (Kneib 2000). Once inside the estuary, fauna must adapt to often rapid changes in salinity, physiochemistry, hydroperiod, nutrient dynamics, and habitat distribution, that is often driven by changes in freshwater inflow. (Browder & Moore 1981).

Climatically-driven changes in freshwater inflow into estuaries affect the salinity, flooding, sediment, nutrient and physiochemical characteristics of the estuary, which in turn may influence species composition, abundance, diversity and distribution (Alber 2002, Kimmerer 2002). For example, Rozas et al. (2005) showed shifts in estuarine nekton community structure after large fluvial pulses from the Mississippi River. Similarly, inflow has been shown to be important in structuring communities of phytoplankton (Yamamoto & Hatta 2004), infauna

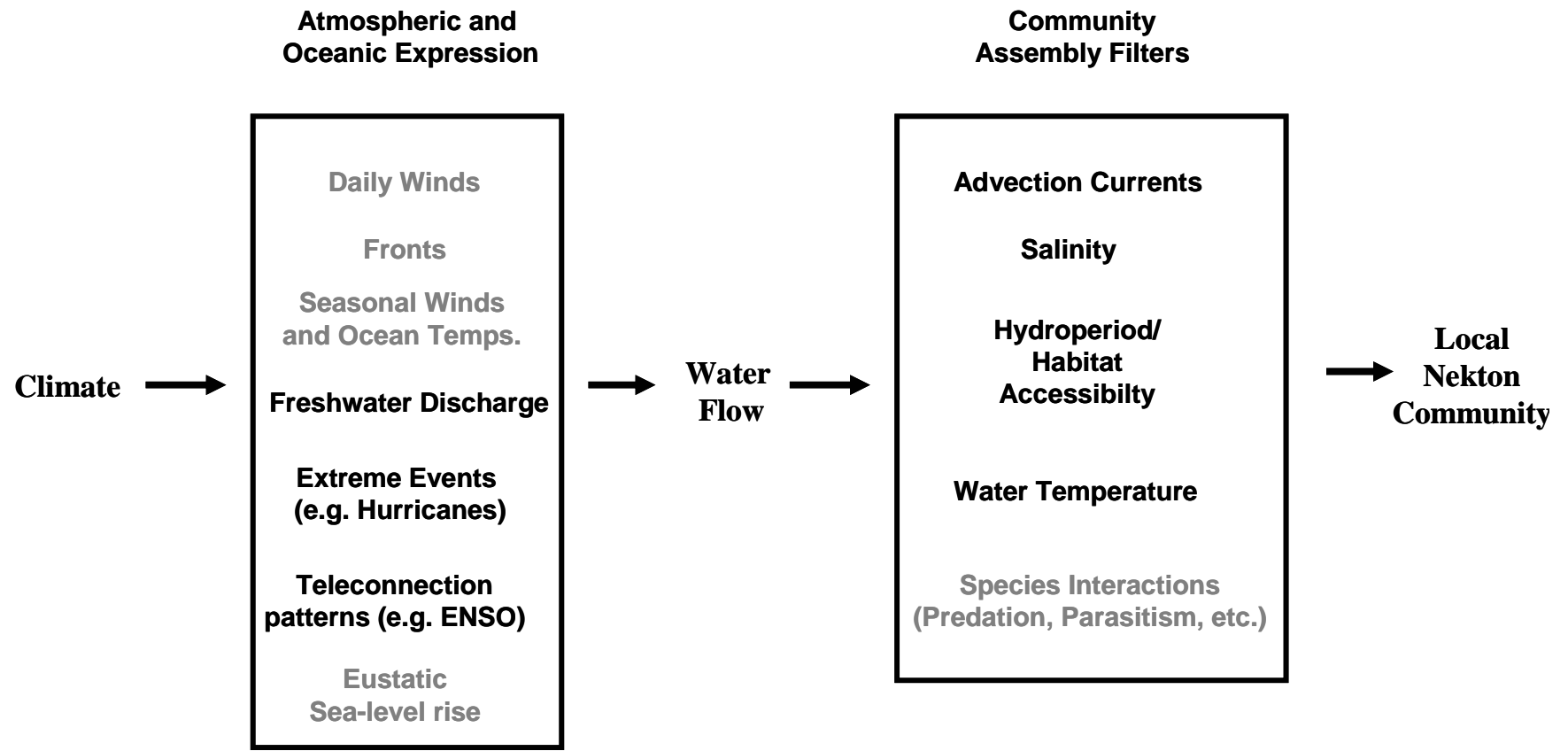


Fig. 1.1. Conceptual model showing how climate controls local estuarine nekton community structure. Items in black were addressed in this dissertation.

(Montagna & Kalke 1992, Montagna et al. 2002), sessile invertebrates (Powell et al. 1992, Kim & Powell 1998, LaPeyre et al. 2003), crustaceans (Little 2000) and fish (Kushlan 1976, Laevatsu 1993, Livingston 1997, Kimmerer et al. 2001, Piazza & La Peyre 2007). Changes in climatically-driven freshwater flooding has the potential to affect estuarine energy transfer through changes in the community dynamics of estuarine nekton, particularly resident species.

Nekton (fish and decapod crustaceans) are important components of the estuarine system and have been hypothesized as being the key to energy transfer from the estuary to the coastal ocean (Turner 1977, Nixon 1980, Boesch & Turner 1984, Kneib 1997, 2000, and others). Through their role as forage species, resident nekton may provide a crucial link in the trophic support of fishery populations, with migratory species in subtidal habitats transferring energy to the coastal ocean (Kneib 1997). Ephemeraally flooded marsh surfaces have been identified as key areas for this trophic exchange (Kneib 1997), as climatically-induced changes in water flow create energetic habitat quality differences. Consequently, climate effects on nekton can often be revealed not only by the presence or absence of certain species (e.g. see Hofmann & Powell 1998, Davis 2000) but also by changes in fish growth (Brandt et al. 2002).

### **RESEARCH OBJECTIVE**

I studied the role of climate in structuring local estuarine nekton communities in Breton Sound estuary, Louisiana. To do this, patterns of local nekton community response to climate variability were investigated in a framework that encompassed multiple spatial and temporal scales and attempted to link critical atmospheric processes with local community assembly filters (Fig. 1.1). Specifically, this dissertation reports on the effects of ENSO-forcing (teleconnection pattern), riverine pulses (freshwater discharge), and marine pulsing from an extreme meteorological event (tropical cyclone). These atmospheric, oceanic, and riverine processes vary

in timing, intensity, and duration; however they all affect potential community assembly filters that structure local nekton communities.

### **STUDY AREA**

Breton Sound (details on the study area, including a map, can be found in the following chapters) likely plays an important role as a nursery for both marine and freshwater species in the northern Gulf of Mexico and is well suited to ecological study of the effects of climate variability at different temporal scales. High natural and anthropogenically-forced land loss rates ( $> 6.7 \text{ km}^2 \text{ y}^{-1}$ ) in the basin prior to the 1990s spurred the building of the Caernarvon Freshwater Diversion (1991), at the apex of the Breton Sound estuary to provide controlled river inflow, moderate salinities and restore fluvial processes to the estuary. Breton Sound contains an extensive and long-term (1988 – present) data set that monitors environmental (water level, temperature, and salinity), meteorological, and biological (nekton) conditions both within and in close proximity to Breton Sound. This data set provided an opportunity to study the effects of ENSO forcing on estuarine nekton. Additionally, a management strategy of annual winter/spring riverine pulsing through Caernarvon provides periodic, discrete, and controlled high-volume fluxes of Mississippi River water ( $184 \text{ m}^3 \text{ s}^{-1}$ ) into the basin to simulate natural variability in flow processes. This management strategy provided the opportunity to investigate the effect of freshwater discharge on estuarine nekton communities.

### **SYNOPSIS OF CHAPTERS**

Chapter two examines whether local estuarine nekton were governed by large-scale climatic forcing. Specifically, I examined whether a teleconnection exists between ENSO and the abundance of juvenile brown shrimp (*Farfantepenaeus aztecus*), a critical commercial species, in Breton Sound estuary. I also related juvenile brown shrimp abundance to ENSO-

forced environmental assembly filters that affect brown shrimp recruitment, survival, and growth in the estuary.

Because climate variability also affects the timing and intensity of riverine flooding in estuaries, in Chapters three and four, I examined the effect of short-term riverine pulsing on estuarine nekton communities and growth. Riverine discharge is a climatically-induced process that has a tremendous effect on estuarine processes and the biotic community. Freshwater inflow is highly variable and affected by climatic processes that may occur a large distance away. Future changes in climate may affect freshwater discharge to estuaries, causing large increases in some areas and decreases in others and significant challenges for planning and ecosystem management (Palmer et al 2008). However, it is little understood exactly how water flow pulses of different timing and duration translate to differences in estuarine productivity. I used the controlled, discrete riverine pulses from Caernarvon to investigate the effects of freshwater discharge on nekton community structure, assembly, and productivity. Chapter four is a report on the effect of short-term riverine pulsing on nekton abundance, biomass, community assembly and biodiversity. Chapter four reports the effect of pulsed riverine flow on nekton growth.

Climate affects the frequency, magnitude, and pathway of tropical cyclones. These extreme meteorological events have the potential to deliver large disturbance and marine pulses to local estuarine habitat. During my field research, Breton Sound received a direct hit from Hurricane Katrina that came ashore as a strong Category 3 (Saffir-Simpson scale) cyclone. This extreme meteorological event caused physical habitat disturbance and a protracted marine pulse that lasted several months. Chapter five is a report of the effect of Hurricane Katrina on nekton communities.

Studying the linkage between climate and nekton provides vital information on estuarine ecosystems and productivity. In Chapter six, I summarize the contribution of this body of



research toward understanding the effects of climate on coastal ecosystems. Additionally, I consider the implications of this research to management of fresh water and restoration of coastal wetlands.

### **LITERATURE CITED**

- Alber M (2002) A conceptual model of estuarine freshwater inflow management. *Estuaries* 25:1246-1261
- Boesch, DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7:460-468
- Bradbury IR, Snelgrove PVR (2001) Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. *Can J Fish Aquat Sci* 58:811-823
- Brandt SB, Mason DM, McCormick MJ, Lofgren B, Hunter TS, Tyler JA (2002) Climate change: implications for fish growth performance in the Great Lakes. *Am Fish Soc Symp* 32:61-76
- Browder JA, Moore D (1981) A new approach to determining the quantitative relationship between fishery production and the flow of freshwater to estuaries. In: Cross R, Williams D (eds) *Proceedings of the national symposium on freshwater inflow to estuaries*, vol. 1. U.S. Fish Wildl Serv, U.S. Dept Int, Washington D.C. p 403-430
- Brown CA, Jackson GA, Brooks DA (2000) Particle transport through a narrow tidal inlet due to tidal forcing and implications for larval transport. *J Geophys Res* 105:24141-24156.
- Cake EW Jr (1983) Habitat suitability index models: Gulf of Mexico American oyster. U.S. Fish Wildl Serv FWS/OBS-82/10.57
- Chesney EJ, Baltz DM, Thomas RG (2000) Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecol Appl* 10:350-366
- Clements FE (1916) *Plant succession: an analysis of the development of vegetation*. Carnegie Institute, Washington Publ No 242
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310
- Darwin C (1859) *The origin of species*. 1998 ed, Wordsworth Editions Limited, U.K
- Davis JLD (2000) Changes in a tidepool fish assemblage on two scales of environmental variation: Seasonal and El Nino Southern Oscillation. *Limnol Oceanog* 45:1368-1379
- Day JW, Jr, Hall CAS, Kemp WM, Yañez-Arancibia A (1989) *Estuarine Ecology*. John Wiley and Sons, New York

- Epifanio CE (1995) Transport of blue crab (*Callinectes sapidus*) larvae in waters off mid-Atlantic states. *Bull Mar Sci* 57:713-725
- Hofmann EE, Powell TM (1998) Environmental variability effects on marine fisheries: four case histories. *Ecol Appl* 8:S23-S32
- Keddy P (1999) Wetland restoration: the potential for assembly rules in the service of conservation. *Wetlands* 19:716-732
- Kim Y, Powell EN (1998) Influence of climate change on interannual variation in population attributes of Gulf of Mexico oysters. *J Shellfish Res* 17:265-274
- Kimmerer WJ, Cowan JH Jr, Rose KA (2001) Analysis of estuarine striped bass populations: Effects of environmental conditions during early life. *Estuaries* 24:557-575
- Kimmerer WJ (2002) Effects of freshwater flow on abundance of estuarine organisms: Physical effects or trophic linkages? *Mar Ecol Prog Ser* 243:39-55
- Klopfer PH (1959) Environmental determinants of faunal diversity. *Am Nat* 94:293-300
- Kneib RT (1997) Early life stages of resident nekton in intertidal marshes. *Estuaries* 20:214-230
- Kneib RT (2000) Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Boston, MA p 267-291
- Kushlan JA (1976) Environmental stability and fish community diversity. *Ecology* 57:821-825
- Laevastu T (1993) *Marine climate, weather, and fisheries*. Halstead Press, John Wiley and Sons, Inc. New York
- LaPeyre MK, Nickens AD, Volety AK, Tolley GS, LaPeyre JF (2003) Environmental significance of freshets in reducing *Perkinsus marinus* infection in eastern oysters *Crassostrea virginica*: potential management applications. *Mar Ecol Prog Ser* 248:165-176
- Little C (2000) *The biology of soft shores and estuaries*. Oxford University Press, New York
- Livingston RJ (1997) Trophic response of estuarine fishes to long-term changes of river runoff. *Bull Mar Sci* 60:984-1004
- Montagna PA, Kalke RD (1992) The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries* 15:307-325
- Montagna PA, Kalke RD, Ritter C (2002) Effect of restored freshwater inflow on macrofauna and meiofauna in upper Rincon Bayou, Texas. *Estuaries* 25:1436-1447

- Montague CL, Ley JA (1993) A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. *Estuaries* 16:703-717
- Nixon SW (1980) Between coastal marshes and coastal waters – a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In Hamilton P MacDonald KB (eds) *Estuarine and Wetland Processes*. Plenum, New York, p 437-525
- Odum WE, Odum EP, Odum HT (1995) Nature's pulsing paradigm. *Estuaries* 18:547-555
- Oliver JE, Hidore JJ (2002) *Climatology: an atmospheric science*. Prentice Hall Inc, New Jersey
- Palmer MA, Reidy Liermann CA, Nilsson C, Flörke M, Alcamo J, Lake PS, Bond N (2008) Climate change and the world's river basins: anticipating management options. *Front Ecol Environ* 6:81-89
- Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. *Am Nat* 100:33-46
- Piazza BP, La Peyre MK (2007) Restoration of the annual flood pulse in Breton Sound, Louisiana, USA: habitat change and nekton community response. *Aquat Biol* 1:109-119
- Rozas LP, Minello TJ, Munuera-Fernandez I, Fry B, Wissel B (2005) Macrofaunal distributions and habitat change following winter-spring pulsed releases of freshwater into the Breton Sound estuary, Louisiana. *Est Coast Shelf Sci* 65:319-336
- Tonn WM (1990) Climate change and fish communities: a conceptual framework. *Trans Am Fish Soc* 119:337-352
- Turner RE 1977. Intertidal vegetation and commercial yields of penaeid shrimp. *Trans Am Fish Soc* 106:411-416
- Turner RE, Brody MS (1983) Habitat suitability index models: northern Gulf of Mexico brown shrimp and white shrimp. U.S. Fish Wildl Serv FWS/OBS-82/10.54
- Weiher E, Keddy P (1999) *Ecological assembly rules: perspectives, advances, retreats*. Cambridge University Press, Cambridge, UK
- Williams LR, Taylor CM, Warren ML Jr, Clingenpeel JA (2003) Environmental variability, historical contingency, and the structure of regional fish and macroinvertebrate faunas in the Ouachita Mountain stream systems. *Environ Biol Fish* 67:203-216
- Yamamoto T, Hatta G (2004) Pulsed nutrient supply as a factor inducing phytoplankton diversity. *Ecol Model* 171:247-270

## CHAPTER 2

### **RELATING LARGE-SCALE CLIMATE VARIABILITY TO LOCAL SPECIES ABUNDANCE: ENSO FORCING AND BROWN SHRIMP (*FARFANTEPENAEUS AZTECUS*) IN BRETON SOUND, LOUISIANA, USA**

#### **INTRODUCTION**

Climate influences local community structure by creating assembly filters that affect the abundance and distribution of species (Tonn 1990, Weiher & Keddy 1999). Assembly filters can be direct or indirect and result from environmental forcing (environmental assembly filters), species interactions, or both (Stenseth et al. 2002). Many studies have linked large-scale climate with effects on plants and animals in terrestrial and aquatic ecosystems largely through the influence of local meteorological parameters and associated environmental conditions (Blenckner & Hillebrand 2002, Stenseth et al. 2002).

Commercial fish stocks are also susceptible to large-scale climate forcing through variability in environmental assembly filters (i.e. water flow, salinity, water temperature) that affect their abundance and distribution (Zimmerman et al. 2000, Garcia et al. 2004, Meynecke et al. 2006). Northern Gulf of Mexico (GOM) estuaries support 66% of the US harvest of penaeid shrimps (*Farfantepenaeus aztecus*, *F. duorarum*, *Litopenaeus setiferus*) and 25% of the US harvest of blue crabs (*Callinectes sapidus*; Zimmerman et al. 2000). While many studies in the region link these species to environmental forcing conditions (salinity, water temperature, water level; i.e. Haas et al. 2001, 2004, Zimmerman et al. 2000, Roth et al. 2008), few link that environmental forcing to large-scale climate processes (but see Childers et al. 1990, Kim & Powell 1998, Soniat et al. 2005, 2009). Given the importance of the GOM to US fisheries and the projected climatic effects on estuarine conditions (e.g. sea-level, river discharge), the ability to predict effects of large-scale climate forcing on commercial fish stocks will be critical for

future fisheries management (Zimmerman et al. 2000, Christenson et al. 2007, Palmer et al. 2008). The objective of this study is to investigate the links between large-scale climate variability and juvenile brown shrimp (*F. aztecus*) abundance in Breton Sound estuary, Louisiana. Specifically, the goals are to 1) determine if a teleconnection exists between local juvenile brown shrimp abundance and the El Niño Southern Oscillation (ENSO) and 2) relate that linkage to environmental assembly filters that may affect juvenile brown shrimp recruitment to and survival in the estuary.

ENSO is one of the most prominent sources of large-scale climate variability worldwide (Glantz 1996, Trenberth & Caron 2000) and refers to the interannual climate signal resulting from atmospheric response to sea surface temperature (SST) fluctuations in the equatorial Pacific Ocean (Trenberth 1997, Trenberth & Caron 2000). During El Niño (the warm phase of ENSO), SST increases in central and eastern portions of the equatorial Pacific. El Niño events are characterized by an atmospheric pressure gradient that decreases from west to east, a corresponding weakening of the easterly trade winds, and increased atmospheric heating in the central and eastern Pacific Ocean. La Niña (the cool phase of ENSO) is characterized by a SST decrease in the equatorial Pacific, causing opposite temperature and pressure conditions from El Niño. ENSO events occur with a periodicity of ca. 3 – 5 y (Graham & White 1988). As a consequence of the variability in atmospheric conditions, ENSO events influence local and regional weather patterns across the globe largely through their effect on the jet stream, cyclogenesis, and the steering of tropical cyclones, and these effects often differ regionally (Ropelewski & Halpert 1987, Noel & Changnon 1998, Trenberth & Caron 2000).

ENSO events have been related to variability in environmental forcing conditions that affect commercially important marine and estuarine species worldwide (Stenseth et al. 2002). The resulting environmental assembly filters have been shown to affect populations of a

commercially important bivalve *Donax dentifer* in Málaga Bay, Colombia (Riascos 2006), Peruvian anchovy off the eastern coast of South America (Stenseth et al. 2002), bigeye tuna (*Thunnus obesus*) in the Indian Ocean (Ménard et al. 2007), skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean (Lehodey et al. 1997), penaeid prawns (Family: Penaeidae) and mullet (*Mugil spp.*) in Australian estuaries (Meynecke et al. 2006), and Eastern oysters (*Crassostrea virginica*) in northern GOM estuaries (Kim & Powell 1998, Soniat et al. 2005, 2009).

ENSO conditions have been related to variability in weather conditions in the southeastern United States (Schmidt et al. 2001, McCabe & Muller 2002). ENSO-related weather effects in this region occur primarily in winter and result from variability in the frequency and intensity of two synoptic weather types – frontal overrunning and Gulf return (McCabe & Muller 2002). El Niño winters are marked by an increase in the frequency and intensity of frontal overrunning conditions, causing cloudiness, cool temperatures, and northerly (offshore) winds. La Niña winters are marked by an increase in the frequency and intensity of the Gulf Return weather type, causing warm, dry conditions, dominated by south and southeasterly (onshore) winds. These differences in regional climate conditions have been related to variability in local sea level (Kennedy et al. 2007), river discharge (Schmidt et al. 2001), water quality (Lipp et al. 2001), and salinity patterns (Schmidt & Luther 2002, Tolan 2007) in northern GOM estuaries.

Brown shrimp (*Farfantepenaeus aztecus*) is one of two commercially important penaeid shrimp species harvested in Louisiana. Like other estuarine-dependent species, brown shrimp are dependent on estuarine nursery areas during the juvenile life stage (Larson et al. 1989, Haas et al. 2004). Adult brown shrimp spawn offshore and larvae are advected to the estuary by near shore currents. Post-larvae settle in the estuary, and juveniles grow rapidly before migrating

back offshore to spawn. Brown shrimp have an annual life cycle, making larval recruitment to the estuary as well as juvenile growth and survival while in the estuary, very important to the year class strength of this important fishery resource (Haas et al. 2001). Therefore, climate-related effects on recruitment, growth, and survival may be important regulators of the fishery. While this recruitment-growth-migration cycle for brown shrimp happens throughout the year, the largest pulse of post-larval brown shrimp settles in Louisiana estuaries during late winter and early spring. It is then, when the effects of potential ENSO-related environmental assembly filters (e.g. river discharge, wind forcing, salinity, water temperature) may affect their abundance and ultimately, their recruitment into the fishery (Haas et al. 2004). As such, this paper addresses the association between juvenile brown shrimp abundance and ENSO and its environmental impacts in Breton Sound, Louisiana.

### **Study Area**

We studied the effect of ENSO on brown shrimp abundance from 1988 – 2007 in Breton Sound estuary, Louisiana (Fig. 2.1). Breton Sound is a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana. It is microtidal and consists of bays, lakes, bayous, canals, and fresh, intermediate, brackish, and saline marsh types. The upper estuary is separated into east and west components, geographically and hydrologically, by Bayou Terre aux Boeufs, a relict Mississippi River distributary. Dominant emergent vegetation in the estuary consists of *Spartina patens* (saltmeadow cordgrass) and *Schoenoplectus americanus* (chairmaker's bulrush) in upper basin marshes, eventually yielding to *Spartina alterniflora* (smooth cordgrass) and *Juncus roemerianus* (black needlerush) in lower basin marshes. The Caernarvon Freshwater Diversion structure (Caernarvon), located at the head of Breton Sound, became operational in 1991 and is capable of delivering substantial amounts of fresh water ( $227 \text{ m}^3 \text{ s}^{-1}$ ) and allochthonous sediments ( $4.5 \times 10^8 \text{ kg y}^{-1}$ ) to the basin (Snedden et al. 2007a). Winter/spring

high-flow freshwater pulsing of the diversion structure began in spring 2001 to simulate seasonal flood-pulse events.

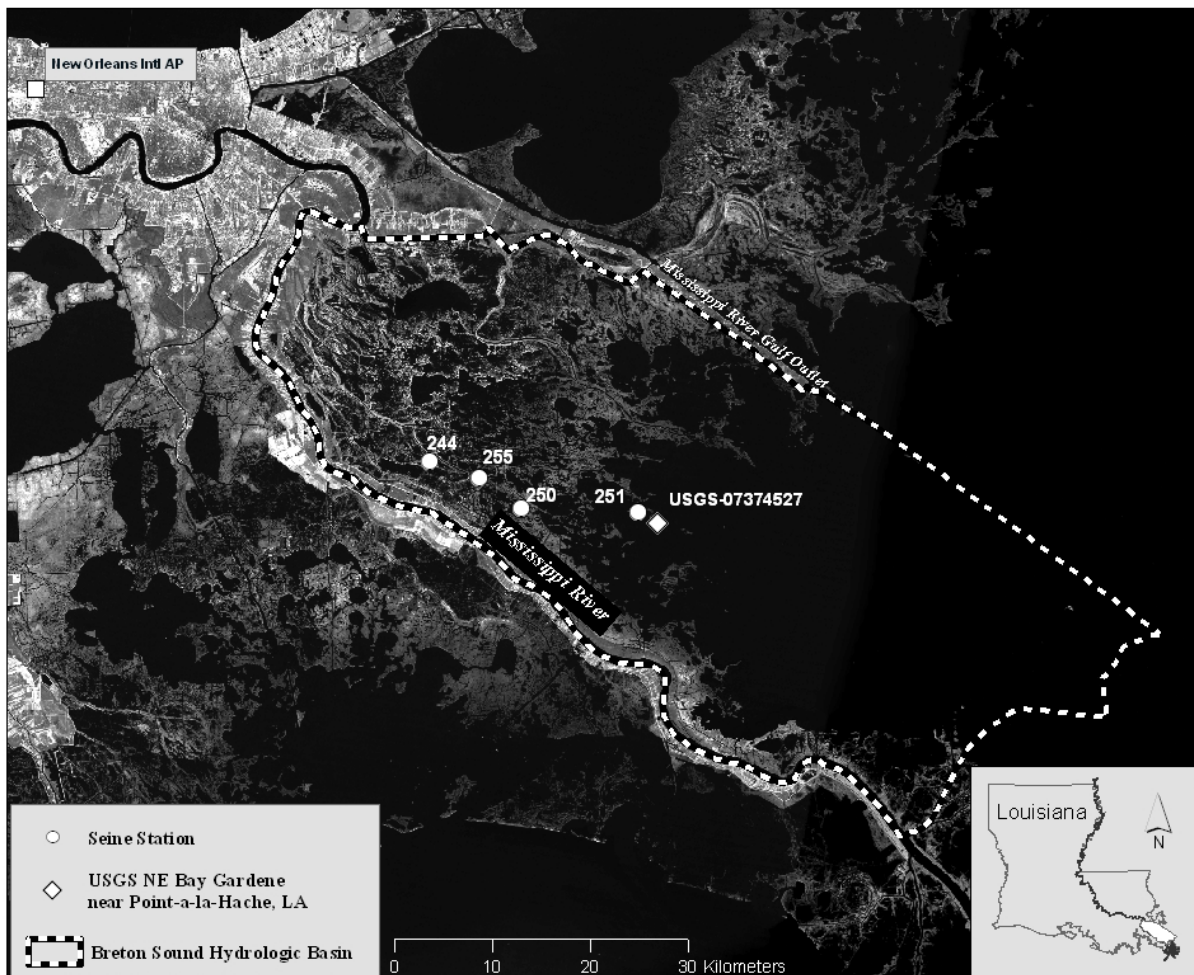


Fig. 2.1. Map of Breton Sound estuary, Louisiana, USA. Dots mark the location of four fisheries independent seine net collection stations used in this study. Triangle marks the location of USGS 07374527 Northeast Bay Gardene near Point-a-la-Hache, LA. Square marks the location of New Orleans International Airport (Sta. Id. 166295).

Pulses release periodic large fluxes of river water into the basin and are capable of inundating upper basin marshes (~ 5,700 ha) for several days (Snedden et al. 2007a,b, Piazza & La Peyre 2007). Without the riverine pulse, inundation of upper basin marshes is dominated by meteorological forcing. Water levels in mid- and lower-basin marshes, as well as in marshes



east of Bayou Terre Aux Boeufs are dominated by meteorological forcing conditions year-round, as is typical in northern GOM estuaries (Rozas 1995, Rozas et al., 2005).

## **METHODS**

### **Data Sources**

#### **Brown Shrimp Abundance Data**

Juvenile brown shrimp abundance was compiled from four fishery independent seine (15 m nylon bag seine; 6 mm mesh) stations in Breton Sound (Station Id: 244, 255, 250, 251; Fig. 2.1). These stations roughly form a west-northwest to east-southeast transect, whereby Station 244 is the northwesternmost station and is located closest to Caernarvon, and Station 251 is the station farthest to the east-southeast, and is situated nearest the GOM. Stations were sampled approximately biweekly from 1988 – 2007 by the Louisiana Department of Wildlife and Fisheries (LDWF). Bag seine stations are used to monitor juvenile finfish, shellfish, and other marine organisms (LDWF 2002), and long-term seine data are a useful index of relative abundance and seasonal/long-term trends. Seine samples were collected over soft bottom areas by attaching 30 m lengths of 1.3 cm nylon rope to each of two 2 m seine pole bridles anchored to the shoreline. After fully extending the line, the seine was fed out parallel to the shoreline. The seine was then hauled in by the two tow lines, and the contents were removed from the bag. Seine samples collected over hard bottom areas were performed by stretching the net and pulling parallel to the shoreline for a distance of approximately 25 m. The outside end was brought toward the shoreline, the net was drawn ashore, and the contents removed (LDWF 2002).

Empirical orthogonal function (EOF) analysis was performed on monthly mean brown shrimp abundance (from each station) as an exploratory tool to examine the spatiotemporal variability in the variable (Emery & Thompson 1998). The analysis showed that abundance and variability in shrimp catch was strongly dominated by station 250. As a result, I normalized the

brown shrimp abundance data to standardize the variance and remove the dominance of station 250. To do this, I subtracted the mean of each station from its value and then divided each by the standard deviation (Burd & Jackson 2002). I then performed an EOF analysis on the normalized abundance, and it revealed that the first mode accounted for almost half (46%) of the variability in the data and showed the basin (all stations) fluctuating in unison. Therefore, I pooled the abundance values for each station and created a combined brown shrimp variable ( $X_{com}$ ) that was computed as follows:

$$X_{com} = \frac{1}{4} \sum X_{sta}$$

where  $X_{sta}$  is the mean monthly value for each station (244, 255, 250, 251). Monthly mean values were then calculated for the new (combined and normalized) brown shrimp abundance variables.

### Environmental Data

Discrete water temperature (°C) and salinity (PSU) measurements were collected at each seine station in Breton Sound in conjunction with biological sampling throughout the entire period of record (1988 – 2007). These discrete measurements were checked against hourly continuous measurements collected at several stations in the basin to ensure that they were accurate indicators of environmental conditions in the basin. The results indicated that the discrete measurements correlated with measurements from all continuous stations. Therefore, the discrete salinity and water temperature measurements were used in the analyses. As with the brown shrimp data, EOF analysis showed a highly significant first mode that dominated the variability for both water temperature (93%) and salinity (82%). This mode for both variables showed the basin fluctuating in unison. Therefore, I pooled water temperature and salinity

values for each station and created combined water temperature and salinity variables, similar to the brown shrimp abundance data, and calculated monthly means for the entire time series.

Hourly real-time water level data were gathered from USGS 07374527 Northeast Bay Gardene near Point-a-la-Hache, LA (1992 – 2007; Fig. 2.1), and monthly mean water level values were calculated for the entire time series.

### Climate and Meteorological Data

The state of ENSO was measured by using the monthly Niño 3.4 sea surface temperature anomaly index for the tropical Pacific rectangle (5° N to 5° S, 170° W to 5° W; Trenberth 1997), taken from the National Weather Service, Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/data/indices/>). The Niño 3.4 index describes SST anomalies relative to a base period climatology and serves as a proxy for the overall ENSO condition (Stenseth et al. 2002). During the 20-year time period of this study, two base periods were used (1961 – 1990 and 1971 – 2000). Months were defined as belonging to El Niño, La Niña, or neutral conditions, based on a five month running mean of the Niño 3.4 sea surface temperature anomaly index (hereafter SSTA). El Niño months exceeded + 0.4 °C. La Niña months exceeded - 0.4 °C, and neutral months fell between  $\pm 0.4$  °C. Monthly ENSO designations were compared against the literature (Trenberth 1997, Lipp et al. 2001, Twine et al. 2005), and there was agreement in the monthly classification.

Hourly real-time measurements of meteorological variables were collected for 1988 – 2007 from New Orleans Louis Armstrong International Airport (Sta. Id. 166295), located approximately 55 km to the northwest of the study area. Variables included atmospheric pressure (mb), precipitation (cm), air temperature (°C), wind speed ( $\text{m s}^{-1}$ ), and wind direction (°). As with the environmental data, these data were checked against shorter time series from continuous recorder stations located in and near Breton Sound, and, like the environmental data,

the measurements from New Orleans airport correlated with measurements from all stations. Therefore, the measurements from the airport were used in the analyses. Monthly mean values were calculated for each meteorological variable. To calculate mean monthly values for wind speed and direction, hourly wind vectors were first rotated to represent a wind blowing toward the direction of the vector ( $^{\circ}\text{T}$ ), and unit vector averages were calculated on the rotated vectors.

### Remote Wind Forcing

Previous researchers have shown that during spring, sea level in Breton Sound is forced by a combination of river discharge (upper estuary) and remote alongshore wind forcing (entire estuary; Snedden et al. 2007b). Remote alongshore wind forcing acts to facilitate estuary-shelf water exchange through Ekman pumping. In Breton Sound, wind stress and coastal sea level are most coherent along the  $110^{\circ} - 290^{\circ}$  component (Snedden et al. 2007b). Consequently, northwest winds (blowing southeastward  $110^{\circ}\text{T}$ ) produce the greatest decrease in estuarine water levels, and southeast winds (blowing northwestward  $290^{\circ}\text{T}$ ) produce the greatest increases in estuarine water levels. Because brown shrimp recruitment is dependent on onshore flow, this information was used to create a wind forcing index that served as a proxy for brown shrimp ‘stocking’ currents. To do this, hourly wind vectors were first rotated to represent a wind blowing toward the direction of the vector ( $^{\circ}\text{T}$ ). Wind vectors were then rotated along the  $110^{\circ} - 290^{\circ}$  component and multiplied by the Cartesian coordinates of the vector to produce a scalar wind speed ( $\text{m}^3 \text{s}^{-1}$ ) along the  $110^{\circ} - 290^{\circ}$  component. Positive values indicate a southeast ‘stocking’ wind (blowing northwestward  $290^{\circ}\text{T}$ ).

### Mississippi River Discharge

Daily Mississippi River Discharge (Q) data were collected for 1988 – 2007 from the station at Tarbert Landing, Mississippi (Gage Id. USACE 01100), and monthly mean values were calculated for the entire time series. This station was chosen because it is upstream from

the Louisiana coastal zone. Therefore, it represents river discharge independent of the effects of local precipitation, runoff, and the effects of flood control projects and freshwater diversions in Louisiana, upstream from Breton Sound.

### **Yearly Anomaly Calculations**

To examine the hypothesis that winter ENSO conditions affect spring abundance of juvenile brown shrimp, I created a winter-spring seasonal subset. For convenience and ease in interpretation, months were further classified into seasons based on the following definitions: winter (January – March) and spring (April – June). I then calculated yearly anomalies for winter and spring seasons (Kimmel et al. 2006). Yearly winter anomalies were calculated for SSTA, meteorological variables (air pressure, air temperature, precipitation, wind forcing), and environmental variables (salinity, water temperature, water level, Q). Yearly spring anomalies were also calculated for the meteorological variables, environmental variables, and juvenile brown shrimp abundance. To calculate the winter anomalies, mean monthly values ( $Y_m$ ) were used to calculate a winter seasonal average:

$$Y_{win} = \frac{1}{3} \sum_{i=Jan}^{March} Y_m$$

where Y is the variable of interest (SSTA, air pressure, air temperature, precipitation, wind forcing, salinity, water temperature, water level, or Q). Next, I calculated

$$Y_{LTM} = \frac{1}{n} \sum Y_{win}$$

where  $Y_{LTM}$  is the long-term arithmetic mean, and n is the number of years (20) in the period 1988 – 2007. The winter anomaly ( $A_Y$ ) was then calculated for each year by using the formula:

$$A_Y = Y_{spr} - Y_{LTM}$$

This process was repeated with the mean monthly spring values ( $Z_m$ ) to calculate a spring average anomaly:

$$Z_{\text{spr}} = \frac{1}{3} \sum_{i=\text{Apr}}^{\text{June}} Z_m$$

where  $Z$  is the variable of interest (SSTA, air pressure, air temperature, precipitation, wind forcing, salinity, water temperature, water level,  $Q$ , or brown shrimp abundance). Next, I calculated

$$Z_{\text{LTM}} = \frac{1}{n} \sum Z_{\text{spr}}$$

where  $Z_{\text{LTM}}$  is the long-term arithmetic mean, and  $n$  is the number of years (20) in the period 1988-2007. The spring brown shrimp abundance anomaly ( $A_Z$ ) was then calculated for each year by using the formula:

$$A_Z = Z_{\text{spr}} - Z_{\text{LTM}}$$

### **Statistical Analyses**

The first step to determine if a teleconnection exists between ENSO and local juvenile brown shrimp abundance was to establish whether ENSO affected meteorological conditions and environmental conditions (potential assembly filters) in Breton Sound. To do this, I used correlation analysis between SSTA (lagged 0–12 months) and monthly meteorological (atmospheric pressure, precipitation, air temperature, wind forcing) and environmental (water temperature, salinity, water level,  $Q$ ) variables. This allowed us to determine the length of ENSO events and their effect on meteorological and environmental conditions. Because ENSO typically affects weather in the southeast US during winter (McCabe & Muller 2002), I also used correlation analysis to assess yearly seasonal relationships between SSTA and meteorological and environmental variable anomalies (winter and spring). Mixed model analysis of variance (ANOVA) was used to investigate differences in yearly winter and spring meteorological and environmental variable anomalies by ENSO category. Least squared means was used to investigate post-hoc differences.

The next step linked juvenile brown shrimp abundance to SSTA and ENSO-related environmental assembly filters. Correlation analysis was used to compare the monthly brown shrimp abundance with the SSTA (lag 0 – 12 months), and stepwise regression analysis was used to explore relationships between monthly brown shrimp abundance and SSTA, meteorological, and environmental predictor variables. To examine the hypothesis that winter ENSO conditions affect spring abundance of juvenile brown shrimp, I repeated the stepwise regression analysis for the yearly data to investigate seasonal effects. I chose stepwise regression to reduce the number of non significant variables in the model. Only variables significant at  $\alpha = 0.10$  were retained in the model (Kimmel et al. 2006). Mixed model ANOVA was used to investigate differences in spring juvenile brown shrimp abundance anomalies by winter ENSO classification. Least squared means was used to investigate post-hoc differences.

The final step in establishing a teleconnection between ENSO and juvenile brown shrimp abundance in Breton Sound was to investigate ENSO-forced environmental assembly filters and potential indirect environmental drivers (i.e. Mississippi River discharge, wind forcing, precipitation). To do this, stepwise regression analysis was used on the yearly winter and spring seasonal data to further explore relationships between significant ENSO-forced environmental assembly filters and seasonal meteorological and environmental forcing. This would reveal any indirect meteorological and environmental forcing effects on brown shrimp abundance. Stepwise regression was used to reduce the number of non significant variables in the model. Only variables significant at  $\alpha = 0.10$  were retained in the model.

## **RESULTS**

### **ENSO**

Analysis of the SSTA shows strong El Niño signals beginning in 1992 and occurring again in late 1997 and 2002 (Fig. 2.2). Strong La Niña signals were present beginning in early

1989, across 1999 and 2000, and in 2007. A total of seven El Niño winters, six La Niña winters, and seven neutral winters were identified from 1988 – 2007 (Table 2.1). Interestingly, of the seven neutral winters, six of them showed positive SSTA, and only one showed a negative anomaly (1997). Correlation analysis between the SSTA index and monthly lagged SSTA suggested that, during the period of record, ENSO event durations were protracted up to nine months (Table 2.2).

### ENSO and Weather

Time series graphs of meteorological conditions are shown in Appendix A. Analysis of the monthly values showed that atmospheric pressure was the only monthly meteorological variable to show a direct significant (negative) relationship with lagged SSTA values (Table 2.2). Precipitation, which was highly correlated with atmospheric pressure ( $p <$

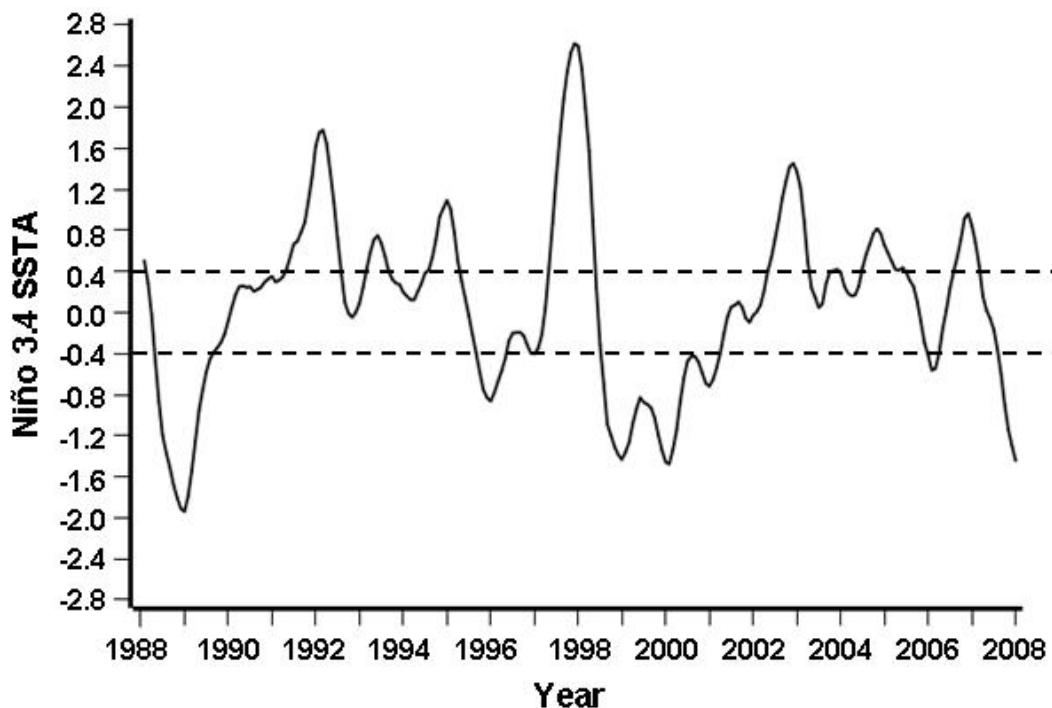


Fig. 2.2. Graph of the five month running mean of the Niño 3.4 sea surface temperature anomaly index. Dashed lines border the neutral classification area. Values above the upper dashed line correspond to El Niño months, and values below the lower dashed line correspond to La Niña months.



Table 2.1. Classification of ENSO events in the winter season (January – March) for the period of record (1988 – 2007) and based on a five month running mean of the Niño 3.4 sea surface temperature anomaly index. Value in parentheses is running mean SSTA value.

ENSO Category	Year
El Niño	1992 (1.72), 1993 (0.41), 1995 (0.76), 1998 (1.98), 2003 (0.86), 2005 (0.50), 2007 (0.43)
La Niña	1989 (-1.52), 1996 (-0.68) , 1999 (-1.23), 2000 (-1.32), 2001 (-0.52), 2006 (-0.50)
Neutral	1988 (0.25), 1990 (0.16), 1991 (0.32), 1994 (0.13), 1997 (-0.18), 2002 (0.01), 2004 (0.20)

0.0001), showed a positive, but non-significant relationship with lagged SSTA values. When viewed by season, winter air pressure ( $r = -0.55$ ;  $p = 0.01$ ;  $N = 20$ ) and temperature ( $r = -0.51$ ;  $p = 0.02$ ;  $N = 20$ ) correlated negatively with SSTA, and winter precipitation ( $r = 0.53$ ;  $p = 0.01$ ;  $N = 20$ ) correlated positively with SSTA. ANOVA results of winter weather patterns by ENSO categories showed negative pressure and temperature anomalies and positive precipitation anomalies during El Niño winters (Fig. 2.3). However, only temperature anomalies differed significantly by Niño category ( $F_{2,17} = 3.50$ ;  $p = 0.05$ ). Mean winter wind direction during the period of record was predominantly from the northeast. Winter wind forcing (velocity along the  $110^\circ - 290^\circ$  component) did not show a relationship to SSTA; however analysis of winter wind forcing by ENSO category showed negative anomalies during El Niño winters and positive anomalies during La Niña winters (Fig. 2.3).

Spring weather patterns (air pressure, air temperature, precipitation) were not correlated with spring ENSO conditions. Spring wind direction during the period of record was mostly from the southeast. Spring wind forcing did not show a relationship to SSTA.

Table 2.2. Pearson ( $r$ ) correlations between Niño 3.4 sea surface temperature anomaly (SSTA) index (lagged 0 – 12 months), brown shrimp (*Farfantepenaeus aztecus*) abundance, and environmental conditions in Breton Sound, Louisiana, USA. Data for SSTA, brown shrimp abundance, salinity, and water temperature are based on N = 240 monthly means. Data for water level is based on N = 192 monthly means. Values in bold are significant at  $\alpha = 0.05$ .

	Niño 3.4 SSTA	Brown Shrimp Abund. (ind)	Weather Variables				Environmental Variables			
			Air Press. (mb)	Precip (cm)	Air Temp. (°C)	Wind Forcing (m s <sup>-1</sup> )	Salinity (psu)	Water Temp. (°C)	Water Level (m NAVD 88)	Q (m <sup>3</sup> s <sup>-1</sup> )
Niño 3.4 SSTA										
Lag 0	-	-0.07	-0.12	0.1	-0.03	-0.04	<b>-0.32</b>	-0.04	<b>0.16</b>	<b>0.14</b>
Lag 1	<b>0.98</b>	-0.09	<b>-0.14</b>	0.11	-0.03	-0.07	<b>-0.35</b>	-0.03	<b>0.18</b>	0.12
Lag 2	<b>0.91</b>	-0.12	<b>-0.15</b>	0.11	-0.04	-0.09	<b>-0.37</b>	-0.03	<b>0.20</b>	0.10
Lag 3	<b>0.82</b>	<b>-0.14</b>	<b>-0.15</b>	0.1	-0.04	-0.09	<b>-0.37</b>	-0.03	<b>0.22</b>	0.08
Lag 4	<b>0.70</b>	<b>-0.16</b>	<b>-0.15</b>	0.11	-0.04	-0.06	<b>-0.37</b>	-0.04	<b>0.24</b>	0.07
Lag 5	<b>0.58</b>	<b>-0.19</b>	<b>-0.14</b>	0.12	-0.03	-0.04	<b>-0.36</b>	-0.04	<b>0.26</b>	0.07
Lag 6	<b>0.45</b>	<b>-0.21</b>	<b>-0.14</b>	0.11	-0.02	-0.01	<b>-0.37</b>	-0.03	<b>0.28</b>	0.06
Lag 7	<b>0.34</b>	<b>-0.22</b>	<b>-0.13</b>	0.1	-0.01	0.02	<b>-0.37</b>	-0.02	<b>0.3</b>	0.06
Lag 8	<b>0.24</b>	<b>-0.22</b>	<b>-0.13</b>	0.08	0.01	0.04	<b>-0.37</b>	-0.01	<b>0.31</b>	0.05
Lag 9	<b>0.15</b>	<b>-0.20</b>	-0.11	0.05	0.02	0.06	<b>-0.35</b>	0.01	<b>0.32</b>	0.05
Lag 10	0.08	<b>-0.18</b>	-0.11	0.02	0.04	0.06	<b>-0.32</b>	0.03	<b>0.33</b>	0.06
Lag 11	0.02	<b>-0.15</b>	-0.1	0.01	0.04	0.06	<b>-0.29</b>	0.05	<b>0.33</b>	0.06
Lag 12	-0.01	-0.12	-0.09	0.003	0.04	0.05	<b>-0.27</b>	0.06	<b>0.32</b>	0.06

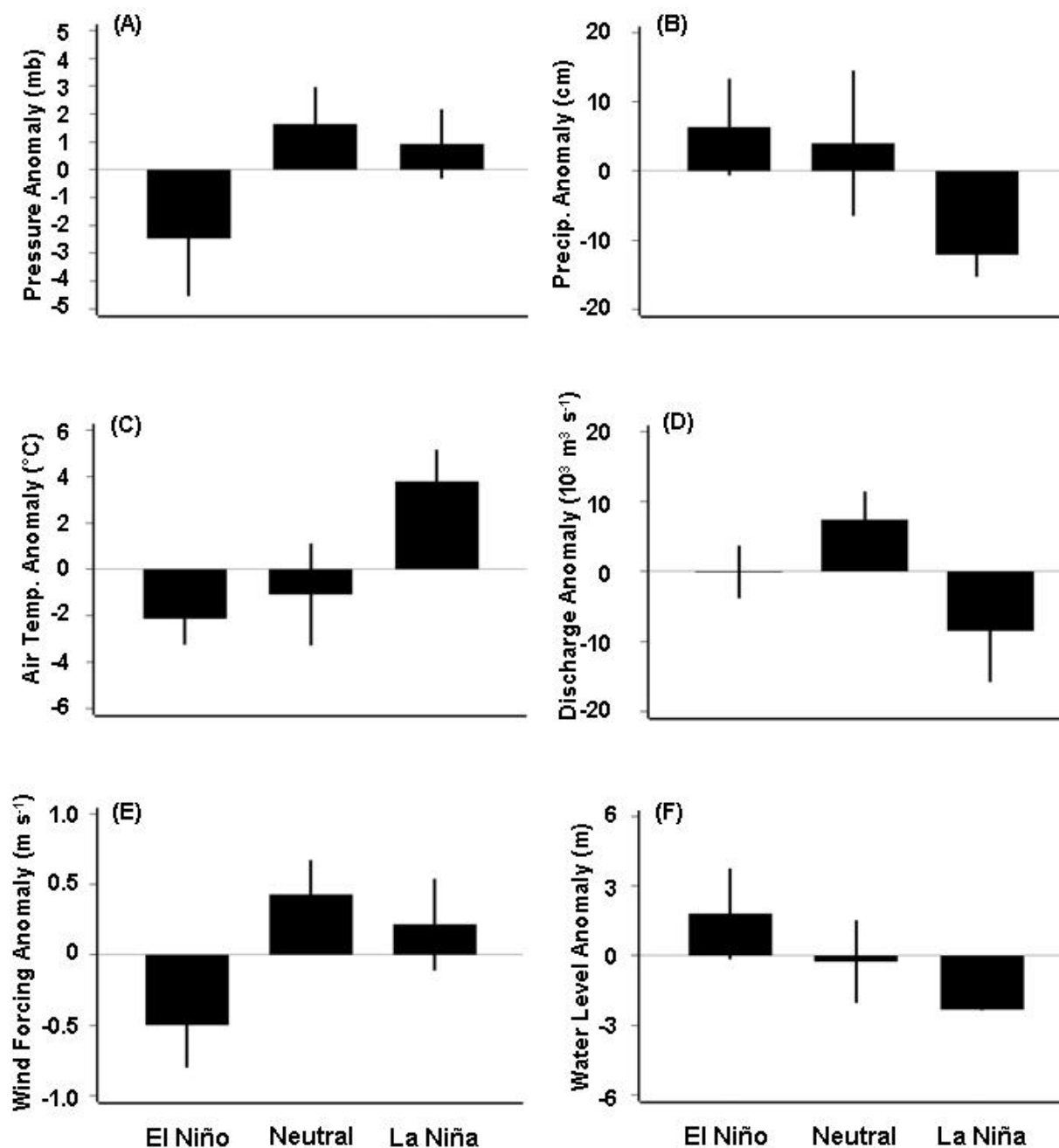


Fig. 2.3. Mean (SE) winter (January – March), (A) surface atmospheric pressure, (B) precipitation, (C) air temperature, (D) Mississippi River discharge, (E) wind forcing, and (F) water level anomalies by ENSO classification. Air pressure, precipitation, air temperature, and wind forcing variables were measured at New Orleans International Airport (Sta. Id. 166295). Mississippi River discharge was measured at Tarbert's Landing, Mississippi (Gage Id. USACE 01100). Water level was measured at USGS 07374527 Northeast Bay Gardene near Point-a-la-Hache, LA. Anomalies for A – E are based on the period of record, 1988 – 2007, and anomalies for F are based on the period of record 1992 – 2007.

## ENSO and Environmental Conditions

Time series graphs of environmental conditions are shown in Appendix A. Mean monthly salinity was lowest at station 244, highest at station 251, and mean water temperature was similar at all stations (Table 2.3). Analysis of the monthly values showed that the SSTA index and all lagged SSTA values correlated significantly with salinity (negative) and water level (positive) in the basin (Table 2.2). There was no direct monthly relationship between SSTA and water temperature. River discharge correlated (positively) immediately with SSTA (Table 2.2). Winter discharge and precipitation anomalies were positively correlated ( $r = 0.44$ ;  $p = 0.05$ ;  $N = 20$ ), and mean discharge anomalies were negative during La Niña winters (Fig. 2.3).

Table 2.3. Monthly mean  $\pm$  SE (range) values of spring (April – June) salinity and water temperature variables as measured at four fisheries independent seine net collection stations (244, 255, 250, 251) in Breton Sound estuary, Louisiana during the period of record (1988 – 2007).

Station	Salinity (psu)	Water Temperature ( $^{\circ}\text{C}$ )
244	$3.2 \pm 0.3$ (0.4 - 8.9)	$26.1 \pm 0.5$ (17.8 - 33.7)
255	$3.7 \pm 0.3$ (0.6 - 9.1)	$26.2 \pm 0.5$ (16.9 - 32.4)
250	$4.9 \pm 0.4$ (1.0 - 11.6)	$26.1 \pm 0.5$ (15.8 - 32.0)
251	$9.1 \pm 0.5$ (2.0 - 19.6)	$25.5 \pm 0.6$ (9.4 - 33.2)

Analysis of the yearly winter-spring relationships showed that winter SSTA correlated significantly (negatively) with spring salinity ( $r = -0.54$ ;  $p = 0.01$ ;  $N = 20$ ), but did not correlate with spring water temperature. ANOVA testing of spring salinity and water temperature anomalies by ENSO categories indicated a significant salinity difference ( $F_{2,17} = 3.50$ ;  $p = 0.05$ )

driven by the pattern of negative spring salinity anomalies following El Niño winters and positive salinity anomalies following La Niña winters ( $t = 3.39$ ;  $p = 0.003$ ; Fig 2.4). Spring water temperature anomalies were near zero following El Niño winters and positive following La Niña winters.

### **ENSO and Juvenile Brown Shrimp Abundance**

Mean juvenile brown shrimp abundance in the seine samples was highest during the spring (April – June; Fig. 2.5). Based on correlation analyses, I identified a significant ENSO signal in brown shrimp abundance at a three month lag, and the negative relationships between SSTA and brown shrimp abundance were protracted for several months (Table 2.2). Stepwise regression showed that monthly brown shrimp abundance could be predicted by the 3 month lagged SSTA [ $BS = -0.10(\text{lag}3) + 0.01$ ;  $r^2 = 0.02$ ;  $p < 0.03$ ;  $N = 237$ ]. When analyzed by year, the winter (January – March) SSTA index did not correlate with spring brown shrimp abundance anomalies for the combined variable or for each station individually. Stepwise regression of the yearly seasonal averages showed that the spring brown shrimp abundance anomaly could only be predicted by spring salinity and spring air temperature [ $bs \text{ anomaly} = 0.37 (\text{salinity}) - 0.39 (\text{air temperature}) - 1.77$ ;  $p = 0.005$ ;  $r^2 = 0.56$ ;  $N = 20$ ]. Examination of the coefficient of partial determination showed that salinity ( $r^2 = 0.36$ ) dominated the relationship. ANOVA of brown shrimp anomalies by ENSO categories showed a pattern of negative spring brown shrimp anomalies following El Niño winters and positive brown shrimp anomalies following La Niña winters (Fig. 2.4). However, this relationship was not statistically significant. Scatter plots of these relationships are shown in Appendix A.

### **ENSO-Forced Environmental Assembly Filters**

Stepwise regression analysis of the yearly spring salinity against all winter and spring meteorological and environmental variables showed that spring salinity was predicted by winter

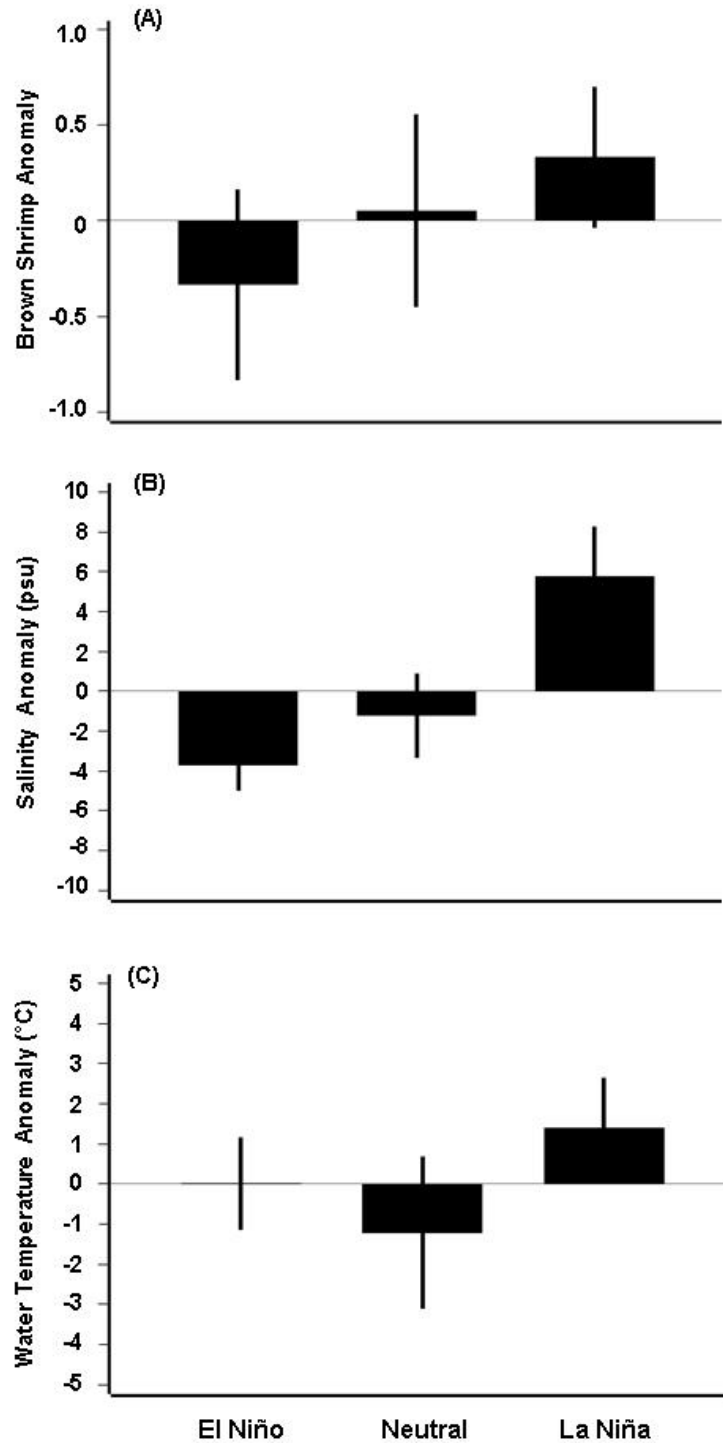


Fig. 2.4. Mean (SE) spring (April – June), (A) brown shrimp, (B) salinity, and (C) water temperature anomalies by ENSO classification, based on the period of record (1988 – 2007). Brown shrimp abundance, salinity, and water temperature variables were measured at four fisheries independent seine net collection stations (244, 255, 250, 251) in Breton Sound estuary, Louisiana. Mean brown shrimp anomalies are based on normalized abundance data.

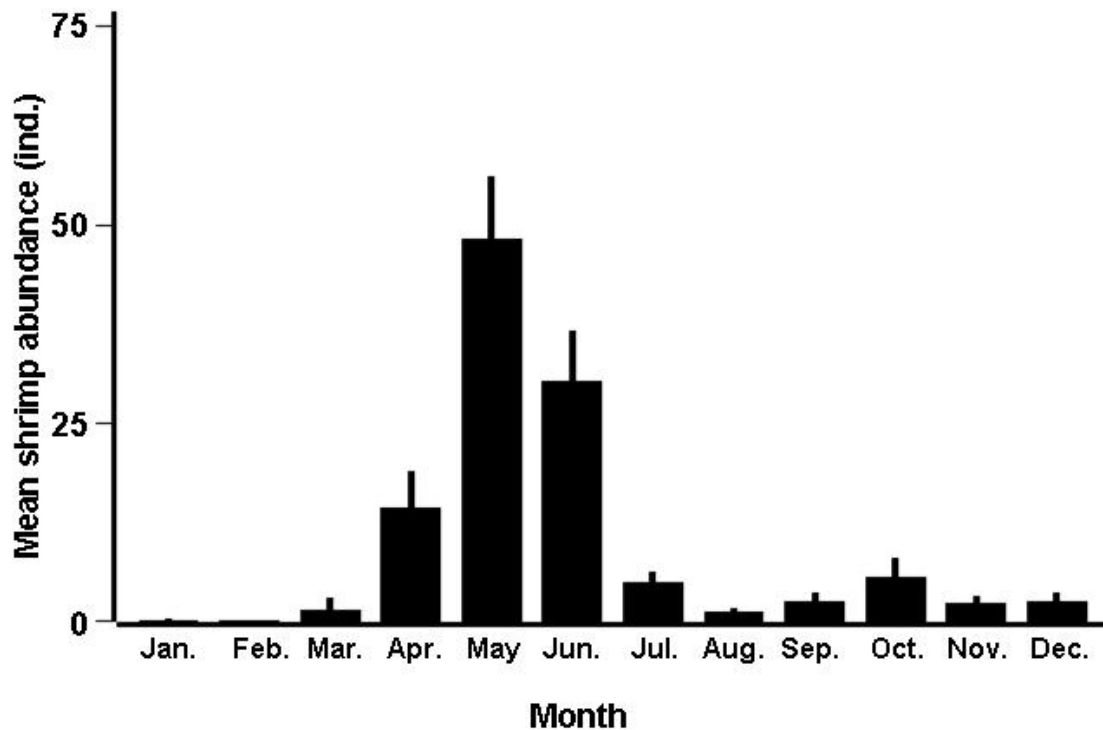


Fig. 2.5. Mean (SE) monthly shrimp catch in seine samples in Breton Sound estuary, Louisiana, USA from 1988 – 2007. Means are based on a combined mean from four fisheries independent seine net collection stations (244, 255, 250, 251).

discharge, spring precipitation, and winter wind forcing [salinity =  $-0.0002 (Q) - 0.10 (\text{precip}) + 2.13 (\text{wind forcing}) + 9.29$ ;  $p = 0.004$ ;  $r^2 = 0.66$ ;  $N = 20$ ]. Examination of the coefficient of partial determination showed that winter discharge ( $r^2 = 0.37$ ) dominated the relationship, followed by spring precipitation ( $r^2 = 0.18$ ) and winter wind forcing ( $r^2 = 0.10$ ).

## **DISCUSSION**

The results identified a teleconnection between juvenile brown shrimp abundance in Breton Sound estuary and the El Niño Southern Oscillation. ENSO affected winter weather conditions (air pressure, temperature and precipitation), and spring brown shrimp abundance in Breton Sound. Juvenile brown shrimp abundance effects lagged ENSO by three months; lower than average abundance of juvenile brown shrimp were caught in springs following winter El Niño events, and higher than average abundance of brown shrimp were caught in springs

following La Niña winters. Salinity was the dominant ENSO-forced assembly filter for juvenile brown shrimp. Spring salinity was cumulatively forced by winter river discharge, winter wind forcing, and spring precipitation.

### **ENSO and Weather**

ENSO effects on winter weather patterns in Breton Sound agreed with those found by other researchers in Louisiana (McCabe & Muller 2002) and the southeastern United States (Ropelewski & Halpert 1986, Schmidt et al. 2001). El Niño winters were marked by lower than normal pressure and temperature and higher than normal precipitation, most likely driven by enhanced formation of winter storms in the GOM, as described by Hsu (1993). Conversely, La Niña winters were marked by positive winter temperature and pressure anomalies and negative precipitation anomalies. These meteorological effects are driven by change in the strength of the subtropical jet stream. The subtropical jet stream increases in strength during El Niño events and decreases in strength during La Niña events. A strengthened subtropical jet stream increases the likelihood of precipitation in the southeastern United States due to a combination of an increase in atmospheric moisture entrainment from the tropics and the southward displacement of frontal systems (Ropelewski & Halpert 1986, McCabe & Muller 2002, Schmidt et al. 2001). Conversely, when the subtropical jet weakens, frontal systems are displaced farther northward, resulting in a decreased likelihood of precipitation.

### **ENSO and Brown Shrimp**

The teleconnection between brown shrimp abundance and ENSO became apparent after three months and its effects were detectable for up to nine months. This result is consistent with research showing that ENSO events typically begin in early winter and peak in strength between three and nine months later (Horel & Wallace 1981). The three-month lagged SSTA was able to predict monthly juvenile brown shrimp abundance, but mean winter SSTA did not directly



predict spring brown shrimp abundance. This lack of predictability in the seasonal data may be an artifact of increased variability in the aggregated data, particularly for juvenile brown shrimp abundance. Although seine data are highly variable (Rozas & Minello 1997), the sampling technique likely did not drive the high variability. Rather, the large variability observed in the abundance data was likely the result of spatiotemporal patchiness in distribution of brown shrimp in the estuary over the 20 y time series. However, even with the high variability in the fisheries data, I was able to identify a teleconnection between ENSO and local brown shrimp abundance that lasted throughout the protracted ENSO events.

### **ENSO-Forced Environmental Assembly Filters**

Estuarine salinity was the dominant ENSO-related environmental assembly filter that affected juvenile brown shrimp abundance in Breton Sound. This finding differs from an earlier study in Barataria estuary, Louisiana (Childers et al. 1990). In that study, brown shrimp harvests (1963 – 1988) were curvilinear, showing lower than normal harvest during both El Niño and La Niña events and greatest harvest during neutral years. I attribute this discrepancy to the difference in assembly filters between the two studies. Childers et al. (1990) concluded that, water level was the dominant environmental assembly filter, with low water level during La Niña events precluding the marsh surface from postlarval settlement. During El Niño events, while water level was high, salinity was lowered, forced primarily by increased local precipitation. Neutral years provided both adequate water level and salinity conditions which enhanced settlement and growth. In this study, water level was related to ENSO conditions; however, it did not appear to directly affect juvenile brown shrimp because, unlike Childers et al.'s (1990) work where the estuary was highly separated from riverine forcing with continuous levees on three sides, Breton Sound is more connected to the Mississippi River. As such, spring water

levels in Breton Sound are typically high; the difference is the component that dominates water levels – fresh or saline water.

Salinity was cumulatively forced by winter river discharge and wind forcing and spring precipitation. Fluvial and atmospheric forcing have been shown to exert strong control over estuarine conditions in Breton Sound (Snedden et al. 2007b). Breton Sound is connected to the Mississippi river in the upper basin via Caernarvon and in the lower basin via overbank flooding. I compared pre- and post-Caernarvon data to determine whether the diversion affected brown shrimp abundance values. While this testing showed no significant Caernarvon effect in the analysis, the combination of restored riverine connectivity and natural flooding can significantly act to freshen the estuary. The results also showed a pattern of more onshore wind flow during La Niña winters and greater offshore wind flow during El Niño winters. This is consistent with the ENSO-related variability in the frequency and intensity of two of the eight synoptic weather types described by Muller (1977), frontal overrunning and Gulf return, that are influenced by ENSO in this region, primarily in the winter (McCabe & Muller 2002). In addition, there is strong linkage between remote atmospheric forcing and coastal water levels in Breton Sound (Snedden et al. 2007b). The linkage of these environmental drivers to salinity suggests both local and regional ENSO control over brown shrimp abundance.

Winter river discharge was related to local winter precipitation (at New Orleans, Louisiana), but the fact that discharge was measured at Tarbert Landing, Mississippi, over 402 river km north of Breton Sound, suggests that that ENSO-forced regional weather patterns, far removed from the estuary, were affecting salinity (by way of dilution from Mississippi River discharge) and local brown shrimp abundance. Local precipitation has been shown to strongly affect river discharge for small rivers in the southeastern US (Schmidt et al. 2001). Mississippi River discharge, however, is often difficult to link to ENSO forcing conditions because the

Mississippi River integrates the response of the water budget across a large region (Twine et al. 2005). Therefore, the effects of ENSO forcing upstream (which may be opposite to that measured in the estuary) are translated to downstream locations, causing different discharge from what is expected (Twine et al. 2005).

Remote alongshore wind forcing is a large-scale process that is vital to estuary-shelf exchange and estuarine circulation in northern GOM estuaries, and specifically Louisiana estuaries, through Ekman processes (Snedden et al. 2007b). Unlike East Coast estuaries, where atmospheric components dominate water levels, microtidal estuaries in the GOM estuaries are heavily reliant on synoptic meteorological forcing to drive coastal water levels and promote estuary-shelf exchange (Rozas 1995). Therefore, wind-driven tides are critical in this region for regulation of estuarine salinity. Additionally, tides are critical for post-larval stocking of many estuarine dependent species (Epifanio 1995, Brown et al. 2000), and brown shrimp are highly dependent on tides to transport them to vegetated marshes where they settle (Zimmerman et al. 2000, Haas et al. 2001, Roth et al. 2008). While the increase in onshore currents earlier in the season may have affected stocking rates, the data were not able to show this connection. To directly assess the effect of this ENSO-forced environmental driver on brown shrimp stocking, it would be necessary to investigate data on postlarval shrimp abundance (i.e. Haas et al. 2001). The results, however, did show that ENSO-forced winter synoptic wind patterns affected salinity and, consequently, juvenile brown shrimp abundance.

ENSO-forced variability in estuarine salinity has been shown to regulate abundance of penaeid prawns in the Gulf of California (Galindo-Bect et al. 2000) and Australian estuaries (Meynecke et al. 2006). Salinity also affects abundance of juvenile brown shrimp in Breton Sound (Rozas et al. 2005) and other Louisiana estuaries (Haas et al. 2001, Roth et al. 2008). However, some penaeid prawns, including brown shrimp, show high physiological resilience to

lowered salinity during the juvenile life stage (Larson et al. 1989, Zimmerman et al. 1990, Galindo-Bect et al. 2000). Therefore, the consistent positive relationship between salinity and brown shrimp abundance may not reflect a direct physiological intolerance to lowered salinity but rather an unmeasured indirect trophic effect of lowered prey items in fresher conditions or, conversely, preference for prey items in higher salinity areas (Zimmerman et al. 1990).

Indirect trophic effects of climate regulation on species abundance through control of the spatial and temporal distribution of prey species have been documented in many habitats (Match-Mismatch Hypothesis; Stenseth et al. 2002). For example, biochemical analysis of lipid tissue has documented opposite population-level responses in pelagic versus demersal fish species in boreal ocean (Gulf of Alaska, Bearing Sea, Scotian Shelf, and North Sea) fish communities and related these to climate-mediated change in essential fatty acid production by phytoplankton (Litzow et al. 2006). Likewise, changes in the abundance of a dominant zooplankton species (*Calanus finmarchicus*) were related to large scale freshening in the Gulf of Maine, as well as to changes in fish community structure (Pershing et al. 2005). While no such indirect prey effects have been uncovered for the northern GOM, three studies in northern GOM estuaries have documented a salinity-moderated teleconnection between ENSO and a common oyster pathogen *Perkinsus marinus* that has large scale indirect effect on oyster populations through regulation of growth and fitness (Kim & Powell 1998, Soniat et al. 2005, 2009).

### **Neutral ENSO Years**

With the exception of atmospheric pressure and wind forcing, winter weather patterns and river discharge during neutral years resembled El Niño years. Similarly, spring salinity and water temperature during neutral years resembled El Niño events. This likely resulted from the fact that six of the seven neutral years had positive SSTA values, two of which (1988, 1991) were close to the cutoff value for classification as an El Niño event. It is interesting that during

neutral years, surface atmospheric pressure and wind forcing, a function of atmospheric pressure (McCabe & Muller 2002) responded in a manner consistent with La Niña events. This is likely because of cyclogenesis, or the lack thereof, during various phases of ENSO. During neutral and La Niña winters, GOM cyclogenesis is less frequent, winds are primarily onshore from the southeast, and regional atmospheric pressure tends to be higher. Conversely, GOM cyclogenesis during winter El Niño events serves to lower regional atmospheric pressure. Since these GOM storms mostly form in the western GOM off the coast of Texas and then track east to northeastward along the GOM coast (Whittaker and Horn 1984), this brings the core of the storm toward the study area, reinforcing the lower pressure locally, as measured at New Orleans.

### **Management Implications**

Although this study did not investigate further the specific mechanisms through which climate affects shrimp populations, the results illuminate an important factor to consider when managing the fishery or restoring coastal wetland habitat. Large winter/spring freshwater releases through the Caernarvon Freshwater Diversion are conducted annually in Breton Sound estuary. These releases are designed to restore the natural flooding conditions that would exist absent the extensive levee system that separates the estuary from the Mississippi River. Often, these freshwater releases are perceived to be at odds with the brown shrimp fishery because of the possible effects on juvenile survival and growth in the estuary. While juvenile recruitment and survival are important to the year-class strength of the fishery resource (Haas et al. 2001, Calliouet et al. 2008), the data indicate that all years are not created equal. This information can assist managers to develop forward-looking strategies that balance the need for fresh water with the needs of the fishery by maximizing potential benefits to each when conditions are conducive. For example, it may not be advantageous to manage for ‘average’ conditions every year, but rather a boom-and-bust method where large freshwater releases are maximized during El Niño

events when shrimp abundance is low and vice versa. Resource managers need to begin incorporating knowledge of climate-induced effects on estuarine resources, especially in the context of future changes in sea-level, river discharge, fishing pressure, and other climatically and anthropogenically-induced environmental conditions.

### **LITERATURE CITED**

- Blenckner T, Hillebrand H (2002) North Atlantic Oscillation signatures in aquatic and terrestrial ecosystems – a meta-analysis. *Global Change Biol* 8:203-212
- Brown CA, Jackson GA, Brooks DA (2000) Particle transport through a narrow tidal inlet due to tidal forcing and implications for larval transport. *J Geophys Res* 105:24141-24156
- Burd AB, Jackson GA (2002) An analysis of water column distributions in Florida Bay. *Estuaries* 25:570-585
- Calliouet CW, Jr., Hart RA, Nance JM (2008) Growth overfishing in the brown shrimp fishery of Texas, Louisiana, and adjoining Gulf of Mexico EEZ. *Fish Res* 92:289-302.
- Childers DL, Day JW, Jr., Muller RA (1990) Relating climatological forcing to coastal water levels in Louisiana estuaries and the potential importance of El Niño-Southern Oscillation events. *Clim Res* 1:31-42
- Christensen JH, Hewitson B, Susuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon WT, Laprise R, Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (2007) Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) *Climate Change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change* Cambridge University Press. Cambridge UK and New York NY, USA
- Emery WJ, Thompson RE (1998) *Data analysis methods in physical oceanography*. 1st ed. Elsevier Science Pub Co, Amsterdam
- Epifanio CE (1995) Transport of Blue Crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. *Bull Mar Sci* 57:713-725
- Galindo-Bect MS, Glenn EP, Page HM, Fitzsimmons K, Galindo-Bect L, Hernandez-Ayon JM, Petty RL, Garcia-Hernandez J, Moore D (2000) Penaeid shrimp landings in the upper Gulf of California in relation to Colorado River discharge. *Fish Bull* 98:222-225
- Garcia AM, Vieira JP, Winemiller KO, Grimm AM (2004) Comparison of 1982-1983 and 1997-1998 El Niño effects on the shallow water fish assemblage of the Patos Lagoon Estuary (Brazil). *Estuaries* 27:905-914

- Glantz MH (1996) Currents of change: El Niño's impact on climate and society. Cambridge University Press, Cambridge, UK
- Graham NE, White WB (1988) The El Niño cycle: a natural oscillator of the Pacific Ocean – atmosphere system. *Science* 240:1293-1301
- Haas HL, Lamon EC III, Rose KA, Shaw RF (2001) Environmental and biological factors associated with the stage-specific abundance of brown shrimp (*Penaeus aztecus*) in Louisiana: applying a new combination of statistical techniques to long-term monitoring data. *Can J Fish Aqu Sci* 58:2258-2270
- Haas HL, Rose KA, Fry B, Minello TJ, Rozas LP (2004) Brown shrimp on the edge: linking habitat to survival using an individual-based simulation model. *Ecol Appl* 1232-1247
- Horel JD, Wallace JM (1981) Planetary-scale atmospheric phenomena associated with the southern oscillation. 109:813-829
- Hsu SA (1993) The Gulf of Mexico – a breeding ground of winter storms. *Mariners Wea Log*, Spring, p. 4-7, 10-11
- Kennedy AJ, Griffin ML, Morey SL, Smith SR, O'Brien JJ (2007) Effects of El Niño-Southern Oscillation on sea level anomalies along the Gulf of Mexico coast. *J Geophys Res* 112:C05047
- Kim Y, Powell EN (1998) Influence of climate change on interannual variation in population attributes of Gulf of Mexico oysters. *J Shellfish Res* 17:265-274
- Kimmel DG, Miller WD, Roman MR (2006) Regional scale climate forcing of mesozooplankton dynamics in Chesapeake Bay. *Estuaries and Coasts* 29:375-387
- Larson SC, Van Den Avyle MJ, Bozeman EL Jr (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) – brown shrimp. *US Fish Wildl Serv Biol Rep* 82(11.90). US Army Corps of Engineers TR EL-82-4
- Lehodey P, Bertignac M, Hampton J, Lewis A, Picaut J (1997) El Niño Southern Oscillation and tuna in the western Pacific. *Nature* 389:715-718
- Lipp EK, Schmidt N, Luther ME, Rose JB (2001) Determining the effects of El Niño-Southern Oscillation events on coastal water quality. *Estuaries* 24:491-497
- Litzow MA, Bailey KM, Prah FG, Heintz R (2006) Climate regime shifts and reorganization of fish communities: the essential fatty acid limitation hypothesis. *Mar Ecol Prog Ser* 315:1-11.
- Louisiana Department of Wildlife and Fisheries (2002) Marine fisheries division: field procedures manual, version 02-1. Louisiana Department of Wildlife and Fisheries, Office of Fisheries, Marine Fisheries Division. Baton Rouge, Louisiana

- McCabe GJ, Muller RA (2002) Effects of ENSO on weather-type frequencies and properties at New Orleans, Louisiana, USA. *Clim Res* 20:95-105
- Ménard F, Marsac F, Bellier E, Cazelles B (2007) Climatic oscillations and tuna catch rates in the Indian Ocean: a wavelet approach to time series analysis. *Fish Oceanogr* 16:95-104
- Meynecke JO, Lee SY, Duke NC, Warnken J (2006) Effect of rainfall as a component of climate change on estuarine fish production in Queensland, Australia. *Est Coast Shelf Sci* 69:491-504
- Muller RA (1977) A Synoptic Climatology for Environmental Baseline Analysis: New Orleans. *J Appl Meteorol* 16:20-33
- Noel J, Changnon D (1998) A pilot study examining U.S. winter cyclone frequency patterns associated with three ENSO parameters. *J Clim* 11:2152-2159
- Palmer MA, Reidy Liermann CA, Nilsson C, Flörke M, Alcamo J, Lake PS, Bond N (2008) Climate change and the world's river basins: anticipating management options. *Front Ecol Environ* 6:81-89
- Pershing AJ, Greene CH, Jossi JW, O'Brien L, Brodziak JKT, Bailey BA (2005) Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. *ICES J Mar Sci* 62:1511-1523
- Piazza BP, La Peyre MK (2007) Restoration of the annual flood pulse in Breton Sound, Louisiana, USA: habitat change and nekton community response. *Aquat Biol* 1:109-119
- Riascos JM V. (2006) Effects of El Niño-Southern Oscillation on the population dynamics of the tropical bivalve *Donax dentifer* from Málaga Bay, Columbian Pacific. *Mar Biol* 148:1283-1293
- Ropelewski CF, Halpert MS (1986) North American precipitation and temperature patterns associated with El Niño/Southern Oscillation (ENSO). *Mon Weather Rev* 114:2352-2362
- Ropelewski CF, Halpert MS (1987) Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Mon Weather Rev* 115:1606-1626
- Roth BM, Rose KA, Rozas LP, Minello TJ (2008) Relative influence of habitat fragmentation and inundation on brown shrimp *Farfantepenaeus aztecus* production in northern Gulf of Mexico salt marshes. *Mar Ecol Prog Ser* 359:185-202
- Rozas LP (1995) Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18:579-590
- Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* 20:199-213



- Rozas LP, Minello TJ, Munuera-Fernandez I, Fry B, Wissel B (2005) Macrofaunal distributions and habitat change following winter-spring pulsed releases of freshwater into the Breton Sound estuary, Louisiana. *Est Coast Shelf Sci* 65:319-336
- Schmidt N, Lipp EK, Rose JB, Luther ME (2001) ENSO influences on seasonal rainfall and river discharge in Florida. *J Clim* 14:615-628
- Schmidt N, Luther ME (2002) ENSO impacts on salinity in Tampa Bay, Florida. *Estuaries* 25:976-984
- Snedden GA, Cable JE, Swarzenski C, Swenson E (2007 A) Sediment discharge into a subsiding Louisiana deltaic estuary through a Mississippi River diversion. *Est Coast Shelf Sci* 71:181-193
- Snedden GA, Cable JE, Wiseman, WJ (2007 B) Subtidal sea level variability in a Mississippi River deltaic estuary, Louisiana. *Estuaries and Coasts* 30:802-812
- Soniat TM, Klinck JM, Powell EN, Hofmann EE (2005) Understanding the success and failure of oyster populations: climatic cycles and *Perkinsus marinus*. *J. Shellfish Res* 83-93
- Soniat TM, Hofmann EE, Klinck JM, Powell EN (2009) Differential modulation of eastern oyster (*Crassostrea virginica*) disease parasites by El Niño – Southern Oscillation and the North Atlantic Oscillation. *Int J Earth Sci* 98:99-114
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science* 1292-1296
- Tolan JM (2007) El Niño-Southern Oscillation impacts translated to the watershed scale: estuarine salinity patterns along the Texas coast. *Est Coast Shelf Sci* 72:247-260
- Tonn WM (1990) Climate change and fish communities: a conceptual framework. *Trans Am Fish Soc* 119: 337-352
- Trenberth KE (1997) The definition of El Niño. *Bull Am Meteorol Soc* 78:2771-2777
- Trenberth KE, Caron JM (2000) The southern oscillation revisited: sea level pressures, surface temperatures, and precipitation. *J Clim* 13:4358-4365
- Twine TE, Kucharik CJ, Foley JA (2005) Effects of El Niño – Southern Oscillation on the climate, water balance, and streamflow of the Mississippi River basin. *J Clim* 18:4840-4860
- Weiher E, Keddy P (1999) Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, UK
- Whittaker LM, Horn LH (1984) Northern hemisphere extratropical cyclone activity for four mid-season months. *J Climatol* 4:297-310

- Zimmerman RJ, Minello TJ, Smith DL, Kostera J (1990) The use of *Juncus* and *Spartina* marshes by fisheries species in Lavaca Bay, Texas, with reference to the effects of floods. NOAA Technical Memorandum NMFS-SEFC-251
- Zimmerman RJ, Minello TJ, Rozas LP (2000) Salt marsh linkages to productivity in of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, p 293-314

## **CHAPTER 3**

### **RESTORATION OF THE ANNUAL FLOOD PULSE IN BRETON SOUND, LOUISIANA, USA: HABITAT CHANGE AND NEKTON COMMUNITY RESPONSE\***

#### **INTRODUCTION**

A general consensus exists among scientists and resource managers that the quantity and timing of freshwater flow to an estuary is central to the maintenance of estuarine resources (Alber 2002). Significant evidence documenting the negative effects of reduced freshwater inflow from human activities such as dams, channels or water withdrawal has led to numerous attempts to restore freshwater inflow, with the goal of enhancing estuarine function (Loneragan & Bunn 1999, Gillanders & Kingsford 2002). In estuaries influenced by large rivers, restoration of freshwater inflow is accomplished largely through the restoration of the annual flood-pulse event. Physical and chemical changes associated with restored freshwater flow can have significant effects on estuarine nekton by inundating the surrounding floodplain and making high-quality habitat available for exploitation (Gillanders & Kingsford 2002). It has been hypothesized that this habitat flooding may be a key factor linking estuaries to high levels of secondary production, and, more recently, that fish may provide an essential link in the movement of energy within and through the estuarine system via the horizontal transport of allochthonous energy off the marsh surface and into subtidal habitats (Kneib 2000). While there have been a number of studies examining the effects of riverine flooding on fisheries of forested floodplain ecosystems (e.g., see Winemiller & Jepsen 1998), few studies in estuarine environments have focused on fisheries-related effects during riverine flood pulses.

Overflow events, common during seasonal flood pulses, transfer large amounts of sediment and nutrients to the floodplain and affect the spatial and temporal variability of

environmental conditions (salinity, sediment, and physiochemistry), which in turn may influence species composition, abundance, distribution and primary and secondary production (Alber 2002). Large freshwater flows, characteristic of flood pulse events, may influence the biotic community structure and production both by positioning dynamic habitat (salinity) relative to static physical habitat (Browder & Moore 1981) and by making ephemeral habitat available for exploitation (Rozas 1995, Kneib 2000). Both mechanisms result in strong associations with fish community structure (Kushlan 1976, Kneib 2000).

Natural delta subsidence and sea level rise coupled with anthropogenic alteration of hydrologic flow regimes, severance of river flooding, and canal dredging have combined to create loss rates in Louisiana of 64 to 91 km<sup>2</sup> per year (Barras et al. 2003). A key component of Louisiana's coastal restoration program involves re-establishing fluvial connectivity to the delta through the construction of 5 active freshwater diversions, ranging in discharge from 7 to 297 m<sup>3</sup> s<sup>-1</sup>. One of the largest diversion projects in Louisiana, the Caernarvon Freshwater Diversion, dramatically influences the supply of fresh water, sediment, and nutrients into the Breton Sound estuary (Lane et al. 2004, Snedden et al. 2007a) and provides a unique opportunity to examine the effects of freshwater flow on estuarine fisheries.

We studied the effects of freshwater pulsing from the Caernarvon structure on estuarine nekton by investigating the ephemeral habitat use resulting from flooding. Specifically, we examined the effects of freshwater flow on estuarine nekton in marsh habitat of the upper Breton Sound estuary, Louisiana during 2 seasonal flood-pulse events in 2005 by comparing nekton abundance, biomass, diversity, and community assembly in treatment (inflow) and reference (no flow) areas.

## **MATERIALS AND METHODS**

### **Study Area**

Breton Sound is a 271 000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana (Fig. 3.1). It is microtidal and consists of bays, lakes, bayous, canals, and fresh, intermediate, brackish, and saline marsh types. The upper estuary is separated geographically and hydrologically by Bayou Terre aux Boeufs, a relic Mississippi River distributary.

This study took place in the upper Breton Sound basin, in emergent marshes subject to flooding from the Caernarvon Freshwater Diversion structure (Caernarvon). Prior to the construction of Caernarvon, the estuary had experienced significant land loss ( $> 18\,000$  ha; Barras et al. 2003) due to isolation from riverine input and natural and anthropogenic habitat alteration (USACE Caernarvon Freshwater Diversion fact sheet; [www.mvn.usace.army.mil/prj/caernarvon/caernarvon.htm](http://www.mvn.usace.army.mil/prj/caernarvon/caernarvon.htm)). Caernarvon became operational in 1991 and was designed to moderate salinities and reintroduce controlled river inflows to Breton Sound. The structure is located at the head of Breton Sound and is capable of delivering substantial amounts of fresh water ( $227\text{ m}^3\text{ s}^{-1}$ ) and allochthonous sediments ( $4.5 \times 10^8\text{ kg yr}^{-1}$ ) to the basin (Snedden et al. 2007a). Dominant emergent vegetation in upper basin marshes consists of *Spartina patens* (Saltmeadow cordgrass) and *Schoenoplectus americanus* (Chairmaker's bulrush).

Yearly experimental high-flow freshwater pulsing of the diversion structure began in spring 2001 to simulate seasonal flood-pulse events and provide opportunity for controlled experimentation. Pulses release periodic large fluxes of river water into the basin and are capable of inundating upper basin marshes ( $\sim 5700$  ha) for several days (Snedden et al. 2007a,b). Without the riverine pulse, inundation of upper basin marshes is dominated by meteorological

forcing as occurs in marshes east of Bayou Terre Aux Boeufs, which are hydrologically separated from diversion flow (Rozas et al. 2005).

### Site Selection

Potential sampling sites (in the inflow and reference areas within the upper 57 km<sup>2</sup> of the estuary) were identified using Digital Ortho Quarter Quadrangle (DOQQ) images and field

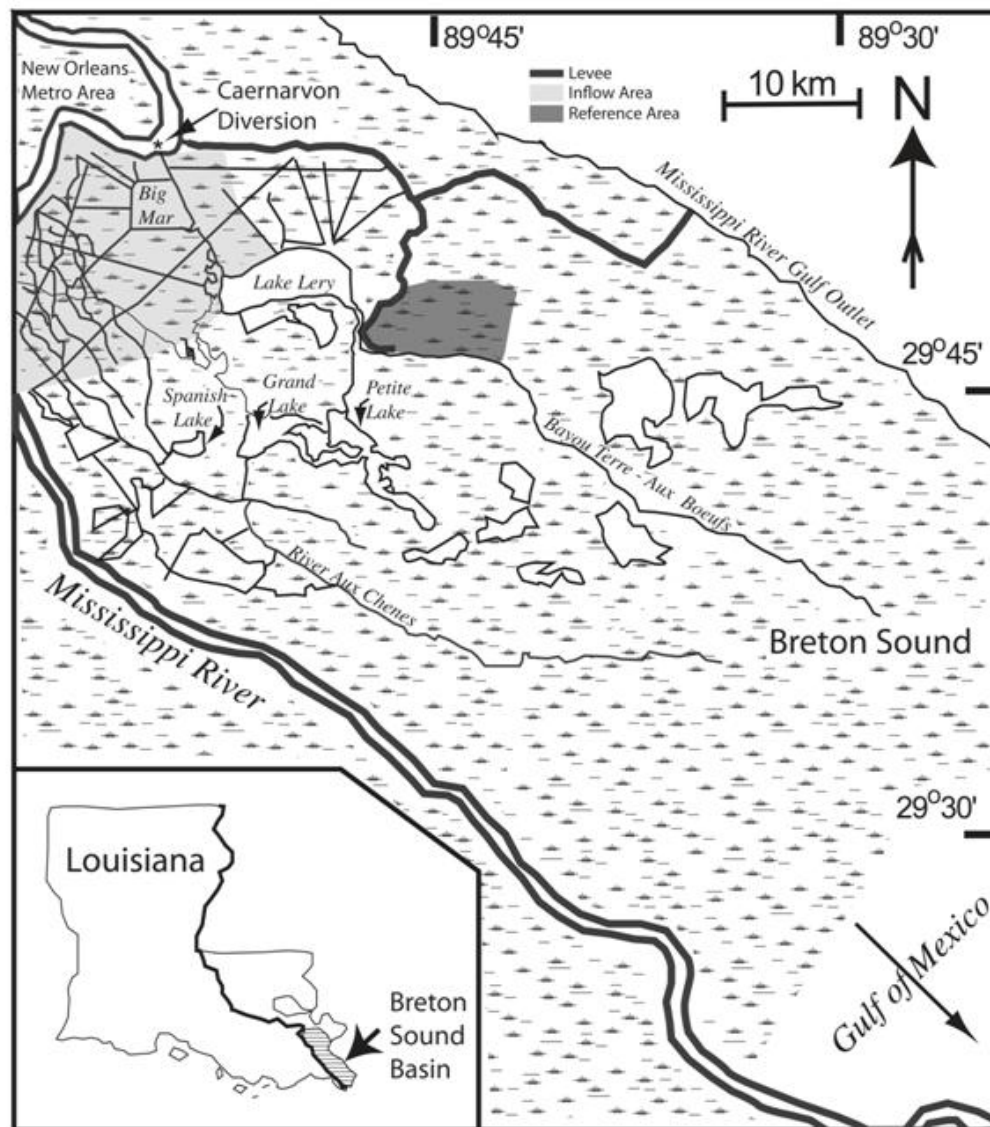


Fig. 3.1. Breton Sound estuary, Louisiana, USA and the location of the Caernarvon Freshwater Diversion. Shaded areas show the locations of the inflow (light gray) and reference (dark gray) areas used in this study. Map is adapted from Snedden et al. (2007b).

reconnaissance. The area west of Bayou Terre Aux Boeufs receives diversion flow and was identified as the inflow area, and the hydrologically separated area east of the bayou was selected as the reference area.

### **Nekton and Environmental Data Collection**

We collected nekton samples in vegetated marsh habitat through both winter/spring pulsed freshwater releases in 2005 (February 14 to 28, March 12 to 28). Sampling was restricted to days when the marsh was flooded, resulting in more sites sampled in the inflow than reference area (Table 3.1). In the inflow area, flooding was a function of the time required for the experimental pulse event to flood the marsh surface. In the reference area, flooding was determined by meteorological conditions and, therefore, occurred less frequently during both pulse events.

Table 3.1. Number of days and sites sampled during both (February 14 to 28, March 12 to 28) Caernarvon experimental high-flow pulse events in 2005. Nekton sampling in both inflow and reference areas was restricted to days that the marsh surface was flooded. Maximum structure discharge during both pulse events was  $184 \text{ m}^3 \text{ s}^{-1}$ .

	February		March	
	Inflow	Reference	Inflow	Reference
Number of days sampled	9	4	9	2
Number of sites sampled	66	18	75	12

Sites were sampled with a 1.14 m cylindrical ( $1 \text{ m}^2$ ) drop sampler. The drop sampler was suspended approximately 3 m from the bow of the boat and 1 m above the marsh surface by a telescoping aluminum boom. A drop sampler was chosen because it provides many advantages for sampling flooded marsh habitat including effectiveness at cutting through underground plant runners, high catch efficiency, and complete enclosure of the water column (Rozas & Minello

1997). In addition, the telescoping boom allowed sampling in the flooded marsh 2 to 3 m from the edge where most nekton biomass on the marsh surface occurs (Kneib 2000). Each sampling site was approached slowly and quietly. The outboard motor was shut off, and the boat was allowed to drift to the vegetated marsh edge. In areas that were too shallow to drift, investigators quietly pushed the boat into position. Once in position, the sampler was dropped and seated securely into the marsh substrate.

After the sampler was dropped, the location of the sampler was logged with a Garmin GPS III, and a suite of environmental variables was collected inside the sampler. Water temperature ( $^{\circ}\text{C}$ ), conductivity (mS), salinity (psu), dissolved oxygen ( $\text{DO}$ ,  $\text{mg l}^{-1}$ ), and pH were measured with a handheld YSI 556 MPS (YSI Environmental). Turbidity (NTU) was measured with a fluorometer (Aquaflour 8000, Turner Designs). Five water depth measurements (mm) were taken inside the sampler with a meter stick, and hourly water depth was downloaded from nearby recorders (Inflow area – USGS 073745253, [http://waterdata.usgs.gov/usa/nwis/uv?site\\_no=073745253](http://waterdata.usgs.gov/usa/nwis/uv?site_no=073745253); Reference area – USGS 073745257, [http://waterdata.usgs.gov/nwis/uv?format=gif&period=31&site\\_no=073745257](http://waterdata.usgs.gov/nwis/uv?format=gif&period=31&site_no=073745257)). Percent cover and species composition of emergent vegetation was visually estimated inside the sampler, and stems were clipped at the substrate and returned to the lab where they were identified and sorted by species and counted.

After environmental variables were measured, nekton inside the drop sampler were collected with 10 successive dip net sweeps (in opposite directions) by 2 investigators concurrently. After dip netting, retained water was pumped through a 1 mm mesh plankton net into a 1 mm mesh cod-end bag (Sea-Gear). Remaining organisms were removed from the marsh substrate by hand. Organisms were preserved in 10% formalin and returned to the laboratory for processing.



In the laboratory, samples were sorted, and nekton were identified to the lowest feasible taxon and counted. Total length of fish, shrimp, and crayfish and carapace width of crabs were measured to the nearest mm. Individuals of each species in a sample were pooled and weighed (g wet weight) to determine biomass.

### **Data Analysis**

Data were tested for normality with the Shapiro-Wilks test. Nekton density and biomass were log transformed to achieve normality. Data are reported as mean  $\pm$  SE, and significance level is reported at  $\alpha = 0.05$ , unless indicated differently.

#### Environmental Variables

Relationships between environmental variables were investigated with correlation analysis. Differences in environmental variables (salinity, DO, temperature, stem density, turbidity, water depth) were compared by treatment (inflow and reference), experimental pulse (February and March), and interactions (treatment\*pulse) using Multivariate Analysis of Variance (MANOVA). Significant MANOVA models were investigated further with univariate ANOVA.

#### Nekton Density, Biomass, Diversity

ANOVA (PROC MIXED) was used to test for statistical differences in density, biomass and diversity between treatments (inflow and reference marsh) and experimental pulses (February and March). Alpha ( $\alpha$ ) diversity was calculated with both Shannon-Wiener diversity ( $H'$ ) and evenness (E). Sorenson's Similarity Index ( $C_s$ ) was used to compare beta ( $\beta$ ) diversity between treatments and pulses.

#### Nekton Communities

The C-score metric (Gotelli 2000) was used to examine community assembly dynamics in flooded habitat. This metric tests for non-random species assembly patterns. Using EcoSim

(Gotelli & Entsminger 2006), we calculated the C-score for an observed presence-absence matrix and tested that value against C-score values resulting from 5,000 random matrix simulations in which species occurrences (row totals) remained fixed and sites (column totals) were equiprobable (SIM2; Gotelli 2000). The SIM2 algorithm was used because it has the lowest incidence of Type I error ( $< 10\%$ ) with field sampling data (Gotelli 2000). Non-significant C-score values for the observed data indicate that species colonized flooded habitat randomly (independent). Observed C-score values that are significantly less than simulated scores suggest more species co-occurrence than expected by chance (species aggregation; Stone & Roberts 1992, Gotelli 2000). Significantly greater C-score values suggest less species co-occurrence than expected by chance (deterministic assembly rules; Stone & Roberts 1992, Gotelli 2000). Investigation of pairwise relationships can identify species pairs that either drive or differ from the suggested co-occurrence patterns (Arrington et al. 2005). Species were included in the C-score analysis if we caught more than 3 ind. in the samples (Gauch 1982). An initial C-score was calculated (1) for the entire data set (all sites), (2) for inflow and reference areas separately and (3) for 2 flooding durations in the inflow area: short (1 to 3 d) and long (7 to 10 d).

Correspondence Analysis (CCA; CANOCO version 4.5; ter Braak & Smilauer 2002) was used to investigate potential associations between taxa and environmental variables at all sites. CCA is a direct-gradient analysis that relates community-variation patterns to environmental variation. Species were included in the CCA if we caught more than 3 ind. in the samples (Gauch 1982). All environmental variables used in the MANOVA were included (salinity, DO, temperature, stem density, turbidity, water depth). Additionally, variables for each month, as well as a 'days flooded' variable were included to investigate timing effects. Environmental variables were tested for significance with 1000 Monte Carlo simulations (CANOCO 4.5; ter Braak & Smilauer 2002).

## **RESULTS**

### **Environmental Variables**

During 2005 experimental pulse events, the marsh was flooded for 69% (February pulse) and 64% (March pulse) of the sampling period in the inflow area and for 31% (February pulse) and 14% (March pulse) of the sampling period in the reference area. Flooding in the reference area was driven solely by meteorological and tidal forcing throughout the study; in contrast, the freshwater inflow obscured tidal periodicity in the inflow area soon after diversion pulsing began (Fig. 3.2). During the February pulse, the inflow marsh was inundated approximately 36 h after the diversion structure was opened. Inflow marshes dewatered completely between pulse events, and in March, marsh inundation began approximately 84 h after Caernarvon was opened.

Results from the MANOVA indicated a significant main-effects model for pulse ( $F_{6,162} = 23.02$ ,  $p < 0.0001$ ) and treatment ( $F_{6,162} = 4.90$ ,  $p = 0.0001$ ). A posteriori tests of main effects showed both pulse and treatment effects for salinity and DO and a Pulse x Treatment interaction effect for turbidity (Table 3.2). Water temperature and stem density showed no significant difference in main effects (Table 3.2). Water depth was positively correlated with stem density ( $p = 0.04$ ) and negatively correlated with DO ( $p = 0.004$ ) at inflow sites. When flooded, mean water depth on the marsh surface was significantly higher at inflow sites than reference sites ( $p = 0.006$ ; Fig. 3.3).

### **Nekton Density, Biomass, and Diversity**

A total of 6521 ind. of 16 taxa were collected. Six resident species (*Palaemonetes paludosus*, *Heterandria formosa*, *Gambusia affinis*, *Lucania parva*, *Poecilia latipinna*, *Cyprinodon variegatus*) comprised 95% of the total abundance (Table 3.3). Density ranged from 0 to 485 ind. m<sup>-2</sup> during the study period. Both density ( $F_{1,153} = 5.35$ ,  $p = 0.02$ ) and biomass

(range 0 to 162.5 g m<sup>-2</sup>;  $F_{1,153} = 8.59$ ,  $p = 0.003$ ) were significantly higher at inflow sites as compared to reference marsh sites (Fig. 3.3).

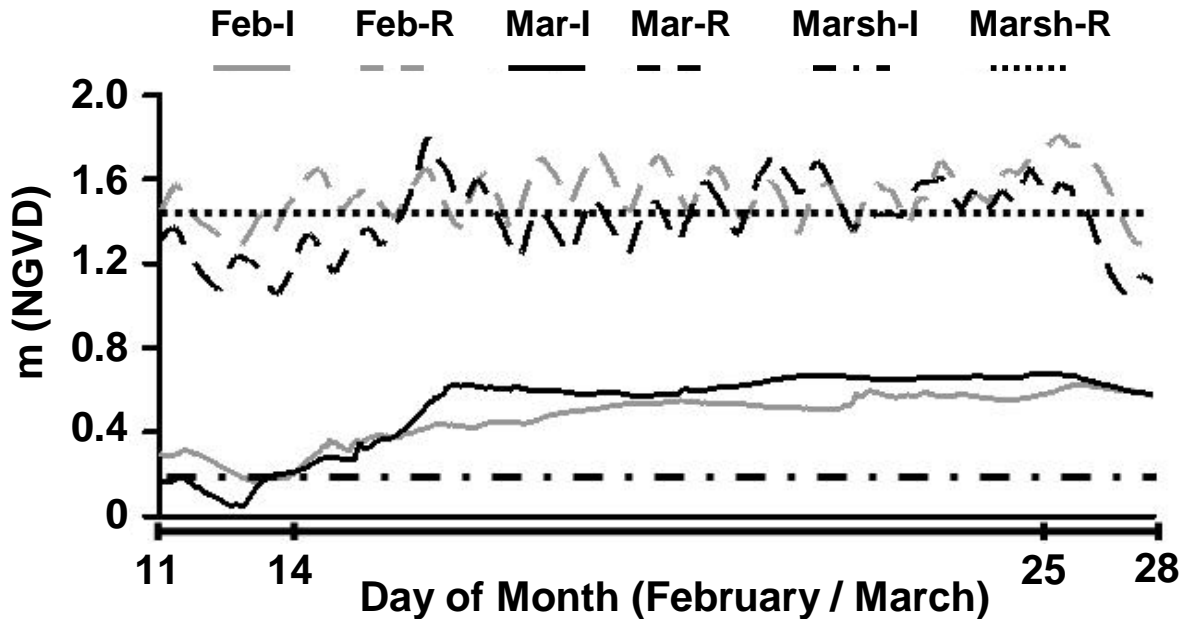


Fig. 3.2. Hydrograph showing water and marsh level before and during both experimental high-pulse flow events in 2005. Pulses dates were February 14–28 and March 12–28. Feb-I: February pulse inflow area; Feb-R: February pulse reference area; Mar-I: March pulse inflow area; Mar-R: March pulse reference area. Source datum for stages and water level in the inflow area was the National Geodetic Vertical Datum, NGVD. Because there was no surveyed water level recorder in the reference area, stages and marsh level were based on an investigator-created datum, transferred from USGS 073745257.

Mean Shannon diversity ( $H' = 0.87 \pm 0.03$  SE) and evenness ( $E = 0.72 \pm 0.02$  SE) did not vary by pulse or treatment (Fig. 3.3). Rank-abundance curves (pooled across both pulses) show that flooded inflow marsh sites were strongly dominated by a single species (geometric pattern of species abundance), while flooded marsh sites in reference marshes were less single-species dominated, showing closer to a log-normal pattern of species abundance (Fig. 3.4). The dominant species at inflow sites switched from *Palaemonetes paludosus* during the February pulse to *Heterandria formosa* during the March pulse (Table 3.3). With the exception of some rare species, assemblages were similar during both 2005 February and March pulses (13 species

Table 3.2. Environmental characteristics of samples in inflow and reference areas during Caernarvon experimental high-pulse flows in 2005. Data for inflow and reference areas are mean  $\pm$  SE (range). Effects — P: pulse; T: treatment. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

Variable	Inflow Area		Reference Area		P	F	
	February (n=66)	March (n=75)	February (n=18)	March (n=12)		T	P x T
Salinity (psu)	0.3 $\pm$ 0.01 (0.2 - 0.7)	0.2 $\pm$ < 0.01 (0.2 - 0.2)	1.0 $\pm$ 0.27 (0.3 - 4.7)	0.7 $\pm$ 0.07 (0.3 - 1.0)	5.4*	16.2***	2.1
Dissolved Oxygen (ppm)	5.7 $\pm$ 0.22 (1.8 - 9.4)	2.2 $\pm$ 0.08 (1.0 - 4.3)	4.4 $\pm$ 0.57 (0.9 - 8.3)	1.8 $\pm$ 0.19 (1.4 - 3.8)	105.3***	6.0*	2.3
Water Temperature (°C)	17.3 $\pm$ 0.35 (11.3 - 23.2)	18.4 $\pm$ 0.50 (10.5 - 28.1)	18.6 $\pm$ 0.31 (15.5 - 21.6)	18.5 $\pm$ 0.84 (15.6 - 24.6)	0.4	1.3	0.7
Turbidity (NTU)	15.9 $\pm$ 1.14 (0.8 - 50.0)	14.9 $\pm$ 1.06 (0.9 - 38.3)	14.1 $\pm$ 3.65 (1.7 - 56.3)	23.7 $\pm$ 5.38 (3.4 - 60.8)	3.8	3.4	5.6*
Stem Density (stems m <sup>-2</sup> )	117.6 $\pm$ 19.12 (0.0 - 618.0)	128.6 $\pm$ 15.77 (0.0 - 449.0)	167.8 $\pm$ 38.63 (0.0 - 512.0)	214.9 $\pm$ 37.72 (54.0 - 402.0)	0.9	0.0	0.4

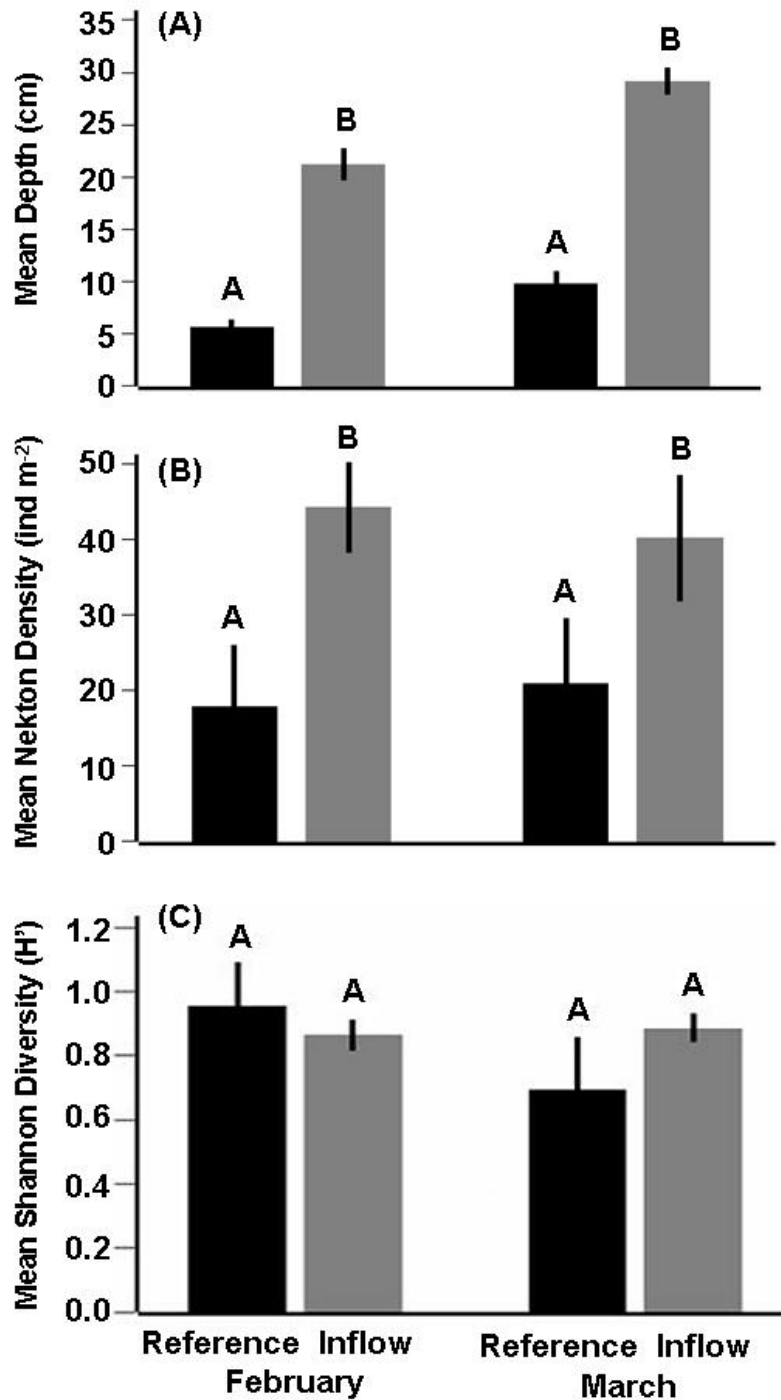


Fig. 3.3. (A) Water depth (cm), (B) nekton density (ind m<sup>-2</sup>), and (C) Shannon-Wiener Diversity (H') at flooded marsh sampling sites during the Caernarvon experimental high-pulse flow events in 2005 (data are mean  $\pm$  SE). Samples — black; reference; grey; inflow. Letters denote significant statistical differences within and between pulse events. Mean biomass (g m<sup>-2</sup>) and mean Shannon-Wiener Evenness, E (both measures not shown) followed the same pattern as density, and, diversity, respectively.

Table 3.3. Mean nekton density (ind. m<sup>-2</sup>) by species during the February and March 2005 Caernarvon experimental high-pulse flow events in Breton Sound, Louisiana, USA. Data are mean  $\pm$  SE. Gray shading indicates the species of highest density by pulse and treatment.

Species	Common Name	Inflow Area		Reference Area		Total Abundance
		February (n=66)	March (n=75)	February (n=18)	March (n=12)	
Fishes (Total=12 sp.)						
<i>Heterandria formosa</i>	Least killifish	9.2 ± 1.9	18.3 ± 6.8	0.1 ± 0.1	0.3 ± 0.2	1,980
<i>Gambusia affinis</i>	Mosquitofish	4.7 ± 1.6	5.7 ± 1.3	4.6 ± 2.1	1.2 ± 0.8	840
<i>Lucania parva</i>	Rainwater killifish	4.6 ± 1.4	0.9 ± 0.2	2.8 ± 2.3	4.6 ± 2.4	483
<i>Poecilia latipinna</i>	Sailfin molly	0.5 ± 0.2	0.6 ± 0.2	3.6 ± 2.1	2.9 ± 1.3	181
<i>Cyprinodon variegatus</i>	Sheepshead minnow	0.4 ± 0.2	0.6 ± 0.2	0.4 ± 0.3	2.4 ± 1.6	107
<i>Fundulus chrysotus</i>	Golden topminnow	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	18
<i>Lepomis macrochirus</i>	Bluegill	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	11
<i>Fundulus pulvereus</i>	Bayou killifish	0.02 ± 0.0	0.01 ± 0.0	0.0 ± 0.0	0.2 ± 0.0	5
<i>Lepomis punctatus</i>	Spotted sunfish	0.04 ± 0.0	0.01 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	4
<i>Lepomis microlophus</i>	Redear sunfish	0.0 ± 0.0	0.03 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2
<i>Anguilla rostrata</i>	American eel	0.02 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1
<i>Notropis</i> spp.	Shiner	0.02 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1
Pooled Fishes		19.7 ± 3.2	26.4 ± 7.9	11.7 ± 5.1	11.7 ± 5.1	3,633
Crustaceans (Total= 4 sp.)						
<i>Palaemonetes paludosus</i>	Riverine grass shrimp	22.7 ± 4.4	11.5 ± 3.3	5.8 ± 3.1	9.1 ± 5.5	2,577
<i>Cambarellus</i> spp.	Crayfish	1.1 ± 0.2	1.3 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	174
<i>Procambarus</i> spp.	Crayfish	0.8 ± 0.2	1.0 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	134
<i>Callinectes sapidus</i>	Blue crab	0.03 ± 0.0	0.01 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3
Pooled Crustaceans		29.3 ± 5.3	14.8 ± 3.4	9.1 ± 5.4	13.8 ± 6.1	2,888

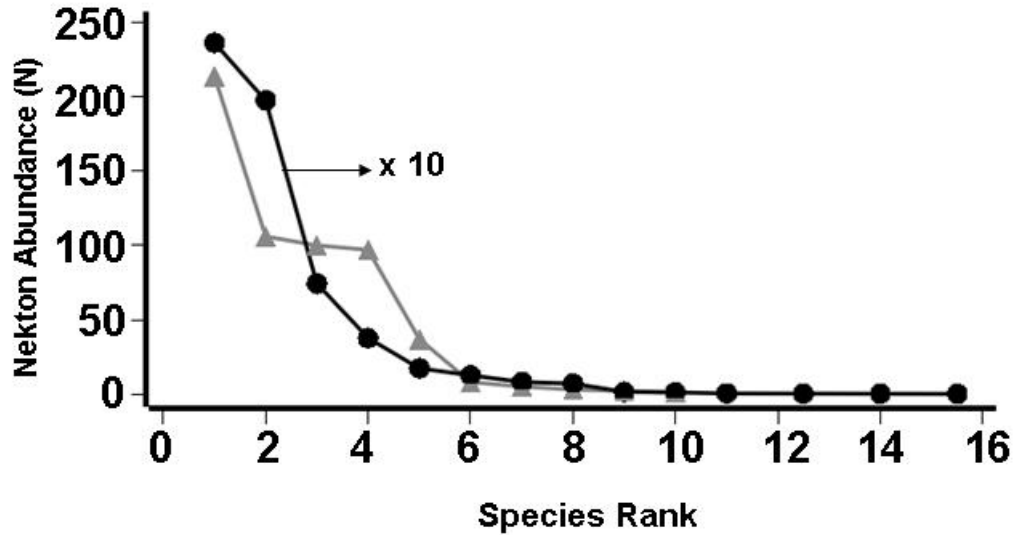


Fig. 3.4. Species rank curves for nekton assemblages caught at flooded marsh sampling sites during the Caernarvon experimental high-pulse flow events in 2005. Samples — black; inflow; grey; reference. Nekton abundance for inflow samples was an order of magnitude higher than the y-axis.

in common;  $C_s = 0.90$ ). Assemblages were less similar between reference and inflow areas (10 common species;  $C_s = 0.77$ ), largely due to the lack of Centrarchids (*Lepomis* spp.) at reference sites.

### Nekton Community Assembly

#### C-score Analysis

Results of the C-score analysis for the entire data set indicated significantly more co-occurrence than expected by chance ( $C_{obs} = 491.9$ ,  $C_{sim} = 608.4$ ;  $p < 0.0001$ ) and were likely largely driven by the dominance of resident species in the assemblages. This relationship was found for both reference ( $C_{obs} = 11.4$ ,  $C_{sim} = 32.0$ ;  $p < 0.0001$ ) and inflow treatments ( $C_{obs} = 491.3$ ,  $C_{sim} = 545.0$ ;  $p < 0.003$ ), as well as for sites continuously flooded for 7 to 10 d during each pulse ( $C_{obs} = 35.0$ ,  $C_{sim} = 43.4$ ;  $p < 0.001$ ). Non-significant C-score values for the observed data were found for sites flooded for short duration (1 to 3 d), indicating random colonization of flooded habitat at those sites. Investigation of pairwise species scores for the entire data set revealed particularly high C-scores for *Palaemonetes paludosus* and *Heterandria formosa* (1000.0), *P. paludosus* and



*Gambusia affinis* (900.0), *H. formosa* and *Poecilia latipinna* (1190.0), *H. formosa* and *Lucania parva* (1325.0), and *L. parva* and *G. affinis* (1598.0), suggesting that, even though these species largely co-exist, they were segregating, at least some of the time.

#### Canonical Correspondence Analysis

Correlation analysis showed a significant positive relationship ( $p = 0.002$ ) between water depth and days flooded. Therefore, only water depth was included in the full model. Forward selection of environmental variables for CCA analysis of all sites showed that water depth ( $F = 21.25$ ,  $p = 0.001$ ), DO ( $F = 5.50$ ,  $p = 0.001$ ), and salinity ( $F = 3.62$ ,  $p = 0.03$ ) were statistically significant. The first two axes represented 94% of the species-environment relationship. Axis 1 was largely a depth axis, correlated positively to water depth (0.64). Axis 2 correlated most strongly with salinity (0.35). DO was influential on both axes (Axis 1 = -0.34, Axis 2 = -0.31). Investigation of the species- environment relationships (Fig. 3.5) shows that a number of the dominant species (*Poecilia latipinna*, *Cyprinodon variegatus*, *Palaemonetes paludosus*, and *Lucania parva*) were associated negatively with depth. *P. latipinna* also associated closely with salinity. Conversely, *Heterandria formosa* associated strongly and positively with depth.

Further investigation of the top 6 species in relation to depth (Fig. 3.6) reveals a difference in abundances with depth. Highest abundances of *Palaemonetes paludosus*, *Lucania parva*, *Poecilia latipinna* and *Cyprinodon variegatus* were found at shallower sites, and both *Gambusia affinis* and *Heterandria formosa* were found in highest abundances at deeper sites.

### **DISCUSSION**

This study documented higher nekton densities and biomasses in marshes receiving high-volume freshwater flow than in marshes not receiving pulsed flow. Differences in density and biomass were attributed mostly to differences in water depth and flooding duration caused by the pulses. Communities were largely similar and consisted mainly of marsh resident species. An

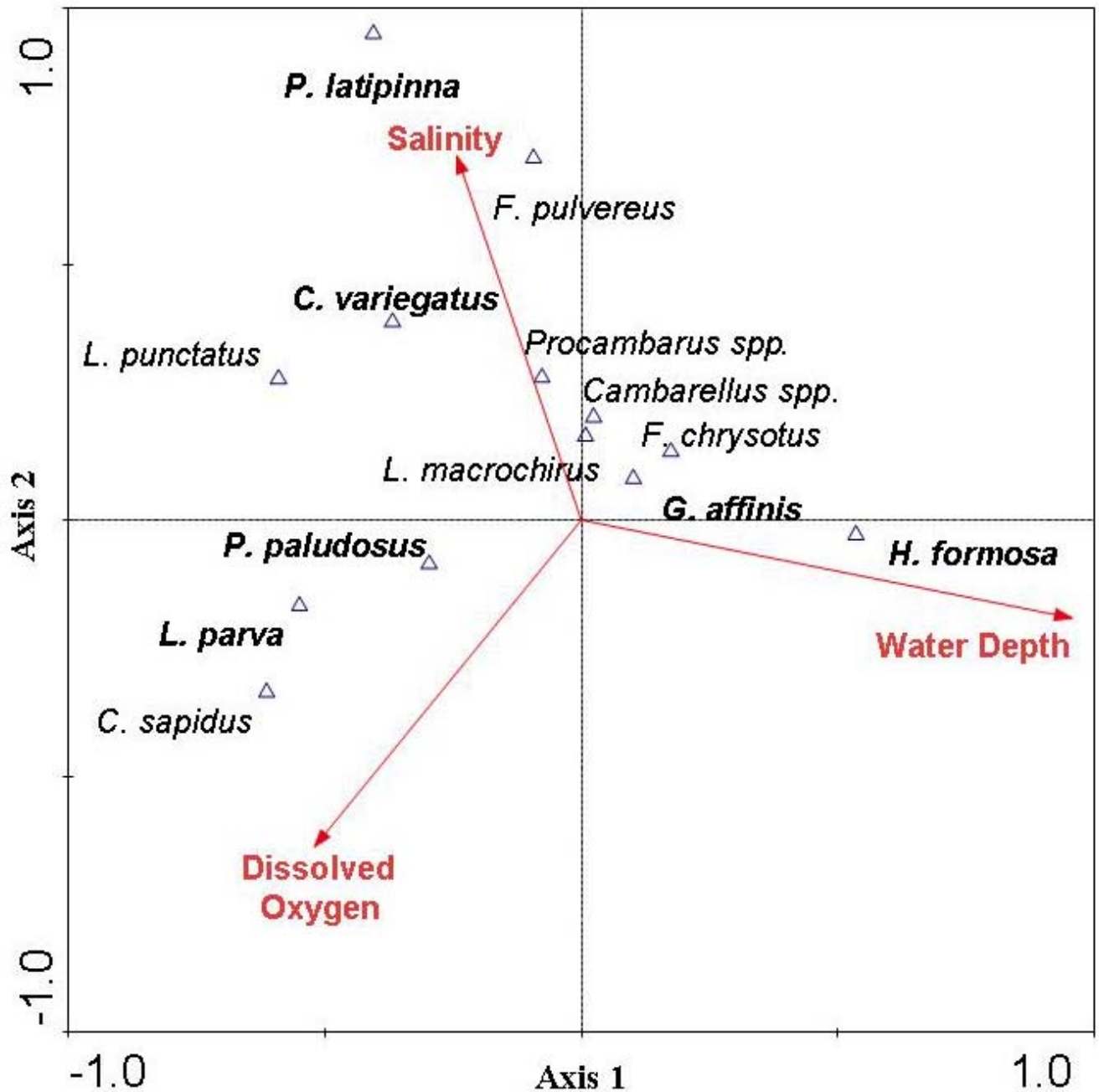


Fig. 3.5. Association of environmental variables and nekton species based on canonical correspondence analysis for all sites in Breton Sound estuary through 2 (February and March) high-flow pulse events of the Caernarvon Freshwater Diversion structure in 2005. Displayed environmental variables are statistically significant at  $\alpha=0.05$ . **Bold**: dominant species (see Table 3 for full names).

examination of individual species also revealed an apparent habitat preference related to water depth.

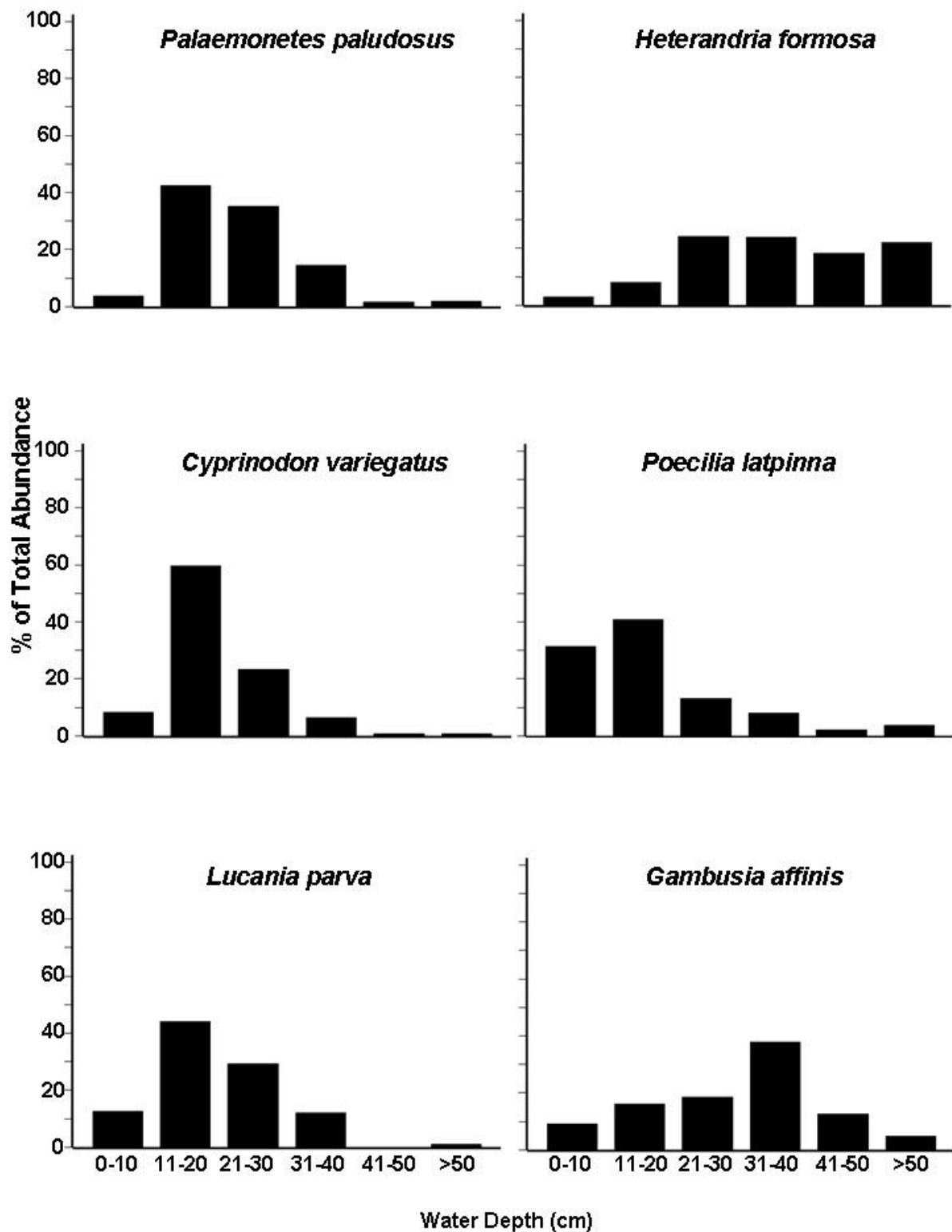


Fig. 3.6. Top 6 nekton species abundances as a function of water depth during Caernarvon experimental pulse events. Samples from all sites (inflow and reference) and pulse events (February and March) were combined.

### **Water Depth and Flooding Duration**

Though marsh inundation events occurred at both the inflow area and the reference area, water depth and inundation periods were greater for marshes in the inflow area during the 2005 experimental freshwater pulses. Throughout Breton Sound, estuarine water levels respond to meteorologically-induced fluctuations outside the estuary over the continental shelf (Snedden et al. 2007b). Fluctuations of this nature comprise most of the subtidal sea level variability in regions outside the diversion's influence. Closer to the diversion, variability attributable to freshwater inputs through Caernarvon exceeds that attributable to meteorological forcing, and this dynamic is reflected in the greater flood durations observed at inflow sites.

Unlike the deterministic semi-diurnal tidal inundation regimes of typical East Coast coastal marshes, flooding events in Breton Sound are driven by relatively stochastic processes that occur over longer timescales: (1) meteorological forcing (4 to 7 d; Chuang & Wiseman 1983); (2) a semi-annual continental shelf sea-level regime that is primarily composed of seasonal patterns in wind forcing and thermosteric sea level fluctuations (Current 1996); and (3) pulsed freshwater releases of Mississippi River water through Caernarvon (14 d). In our study, these pulses of river water contributed to inundation times in the inflow area that were twice that observed in the reference area, as well as provided enhanced nekton access to marsh overflow habitats, and increased the potential residence time in these habitats. Nekton do not appear to be negatively impacted by the relatively stochastic flooding regime as some of the highest densities of estuarine nekton in North America are reported for Gulf coast estuaries (Rozas 1995). This may be due to the fact that once on the marsh surface, nekton can occupy the habitat for long periods of time.

## Nekton Densities

Increased flooding depth and duration at inflow marsh sites were associated with higher densities ( $> 40 \text{ ind. m}^{-2}$ ) than reference marsh sites ( $\sim 15 \text{ ind. m}^{-2}$ ) in our study, and in comparable studies of nekton densities in flooded marsh habitat (i.e., Rozas et al. 2005). When comparing studies, the effects of (1) location, (2) timescale of flooding (i.e. prolonged river-induced vs. diurnal flooding), (3) timing, and (4) gear-type (abundance vs. density) all need to be considered. The closest comparable study (Rozas et al. 2005) used a drop sampler in Breton Sound to investigate pulsing effects from Caernarvon and found total mean nekton densities of approximately  $20 \text{ ind. m}^{-2}$  in vegetated shoreline habitat downstream (inflow area) from the Caernarvon diversion in May 2001, following pulsed freshwater releases earlier in the season. Rozas et al. (2005) primarily investigated salinity effects of pulsing and took place farther down basin than our study and at a time when marsh flooding was largely forced by meteorological tides. In another Louisiana study, Castellanos & Rozas (2001) used a  $1 \text{ m}^2$  throw trap and found densities of over  $30 \text{ ind. m}^{-2}$  at sites vegetated with *Schoenoplectus americanus* in flooded backmarsh habitat on the Atchafalaya River delta. Because their study took place during summer, a time when Atchafalaya River discharge is typically low, the effects of pulsed freshwater delivery were not examined. Rather, their study focused on tidal flooding by marine processes (Ekman transport and thermal expansion of water). In Georgia, Kneib (1997) used simulated aquatic micro-habitats to collect nekton during ebb tides in flooded saltmarsh sites on Sapelo Island. He reported mean densities of  $11.7 \text{ ind. m}^{-2}$  and estimated densities of marsh residents ranging from  $1.8$  to  $16.7 \text{ ind. m}^{-2}$  in flooded intertidal marsh sites. In 2 studies using a  $1\text{-m}^2$  throw trap in the Florida Everglades, Green et al. (2006) reported mean densities of  $6.6 \text{ ind. m}^{-2}$  at freshwater sites in the Taylor River drainage, and Williams & Trexler (2006) documented

mean fish densities of 21.6 ind. m<sup>-2</sup> (range 5.0 to 42.0 ind. m<sup>-2</sup>) in freshwater marsh during the wet season (June to September).

Because our study took place during late winter and early spring, the link between riverine input and nekton densities is more apparent. Studies that track nekton densities during this time of year in the Gulf of Mexico (i.e. February, March) are rare, as most, such as those mentioned above, examine the period from late spring to early fall, when nekton densities on the marsh are typically highest. However, studies that have tracked abundances throughout the year typically found that relative abundances were lowest during the late winter/early spring. For example, one study found that individuals captured during February and March comprised only 2.5% of the annual catch (Kneib 1997), and considering the reported annual mean for that study was 11.7 ind. m<sup>-2</sup> in flooded saltmarsh sites, this represents very low mean densities during early spring. The low densities reported by Kneib (1997) may have been an artifact of lower water levels and nekton aggregation in deeper and warmer habitats.

In our study, flooded marsh sites downstream from the diversion had higher nekton densities and biomasses than flooded marsh sites not receiving diversion flow, possibly due to greater access (i.e. water depth and duration of flooding) to the marsh surface in the inflow area. This finding is consistent with other studies that investigated effects of freshwater flow on estuarine fauna. Montagna & Kalke (1992) found that average density and biomass of benthic macrofauna in samples in the Guadalupe Estuary (high freshwater input) were significantly higher than those in the Nueces Estuary (low freshwater input), and differences in species assemblages in these Texas (USA) estuaries corresponded to freshwater inputs. In Brazil, Barletta et al. (2005) found highest mean values for nekton density and biomass in upper Caeté River estuary sites during the rainy season when freshwater inputs were highest.

## **Nekton Diversity and Community Assembly**

The number of species caught in our study was relatively low for this habitat type, likely due to the time of year. In comparison with other studies of tidal freshwater marsh during peak seasons (e.g. Rozas & Odum 1987, Castellanos & Rozas 2001, Green et al. 2006), we caught about half the number of species and lacked transient species that occupy the marsh surface later during the season. The resident species in our study comprise a guild of omnivores that rapidly colonize the marsh surface once it is inundated, feeding on detritus, epiphytic bacteria, insect larvae, and infauna (Kneib 1997, 2000). These species potentially derive a significant growth and safety benefit by quickly colonizing and remaining on the flooded marsh surface. Within a guild, there is often competition for similar food supplies (Stone & Roberts 1992). However, results of the C-score tests indicated that deterministic processes (e.g. competition) were not affecting community assembly. Rather, our results support the coexistence principle (Stone & Roberts 1992), which states that ecologically closely related species derive benefit from coexistence that outweigh the costs imposed by high within-guild competition for resources. Therefore, ecologically-related species should be found at the same sites more often than by chance. Interestingly, even within this guild that presumably benefits from coexistence, there was evidence of species stratification, and the discriminating factor appeared to be water depth.

Between treatments, assemblage differences were largely due to the lack of predatory species (*Lepomis* spp.) at flooded reference sites. This may be due to the lack of consistent flooding, shallow water depth, and short flooding duration at reference sites, which did not allow time for predator colonization of the marsh surface. Rypel et al. (2007) examined predation risk for a highly motile prey fish species in relation to water depth in Bahamanian tidal creeks and classified a zone of prey refugia (0 to 19 cm), where prey were eaten by predators only 2% of the time, as compared to their deepest sites where prey were eaten 100% of the time (> 70 cm).

Although their depth zones are not directly comparable to our study, what is clear is that depths recorded in flooded reference marshes in our study were likely too shallow for occupation by predatory fishes, while water depths in flooded inflow marshes may have become deep enough to enhance predator colonization, but few were found, even at the deepest sites. Perhaps in our study, predators avoided the deepest sites because deeper sites had more emergent vegetation, and foraging efficiency of piscivores can be limited by dense vegetation (Ruiz et al. 1993).

Several studies have investigated habitat selection of estuarine nekton in relation to water depth and have concluded that nekton assembly to the marsh surface is non-random and may be driven by biotic interactions (Ruiz et al. 1993, Bretsch & Allen 2006a,b). In a study in a South Carolina (USA) salt marsh, Bretsch & Allen (2006a) found that peak flood migration for resident species occurred at depths under 40 cm, and peak migration for the two most abundant residents (*Palaemonetes pugio* and *Fundulus heteroclitus*) occurred between 10 to 20 cm water depth. Assembly of residents in our study was largely similar, as peak abundance for 5 (*P. paludosus*, *Cyprinodon variegatus*, *Poecilia latipinna*, *Lucania parva*, *Gambusia affinis*) of the 6 dominant residents was found at water depths under 40 cm. Of these 5 species, *G. affinis* abundance was different and peaked at the deep end of this range. Although our study did not investigate possible mechanisms controlling habitat selection, avian predation has been cited as a possible factor in selection for deeper habitat by prey fish, especially larger-bodied species (Bretsch & Allen 2006a,b). It is also possible that *G. affinis* selected deeper water depths for breeding. Ruetz et al. (2005) reported a synchrony of assembly with depth for *G. holbrooki* and attributed it to *in situ* breeding, rather than dispersal. This mechanism also could explain the strong assembly pulse at deep water sites shown by *Heterandria formosa*.

*Heterandria formosa* was consistently found in large numbers ( $> 30 \text{ ind. m}^{-2}$ ) at deeper water sites ( $> 50 \text{ cm}$ ), suggesting a possible coupling of this species with freshwater pulsing.



These densities were very high as this species is not usually numerically dominant in Louisiana studies (e.g. see Castellanos & Rozas 2001). However, this colonization pattern agrees with those found for *H. formosa* in the Florida Everglades, where this species recovers slowly after marsh drydown events and is consistently more abundant at long-hydroperiod sites than at short-hydroperiod sites (Trexler et al. 2002, DeAngelis et al. 2005, Ruetz et al. 2005). Seasonal timing did not appear to be a factor in the abundance pattern because we did not see a similar pulse in *H. formosa* abundances in the reference area that mirrored the inflow area. In fact, *H. formosa* was completely absent from reference sites during February and was also largely absent from reference sites during the March pulse. Additionally, observations of this tiny fish species at deep water sites does not agree with work that shows positive relationships between body size and depth for estuarine resident and transient fish species (Bretsch & Allen 2006 A), which suggests predation as a dominant control factor. More likely, this assembly pulse of *H. formosa* at deep water sites in the inflow area may signify a coupling between freshwater pulsing and breeding that is attributable to the increased depth and duration of flooding in the inflow area. Although we did not study this mechanism, phenotypic plasticity in breeding behavior is commonly seen in variable environments (Schaffer 1974) and specifically in Poeciliidae (Thibault & Schultz 1978). Additionally, in the Everglades, population dynamics of *H. formosa* were attributed to a Moran effect, synchronized by water depth, and recolonization of this and other Moran-controlled species (e.g. *Gambusia holbrooki*) was attributed to *in situ* reproduction and not dispersal (Ruetz et al. 2005).

Our results suggest that freshwater pulsing may enhance secondary productivity in the Breton Sound estuary; increased nekton density, biomass and community assembly were directly attributed to factors associated with marsh surface flooding. However, when reporting results such as these, the question always arises whether increased abundances are the result of

increased habitat availability (build it and they will come) or because of increased habitat quality (e.g., nutrient enrichment) from riverine input. In the case of Breton Sound, evidence has been reported for both rapid uptake of nutrients (N and P; Lane et al. 2004) and transfer of the riverine nutrients into resident species (*Palaemonetes* spp.) downstream from pulsed riverine input (Rozas et al. 2005). Additionally, in our study, we repeatedly observed red drum *Sciaenops ocellatus*, a predator, swimming along flooded marsh edges in fresh water directly downstream from the diversion. The presence of upper trophic level predators such as red drum in these areas suggests a benefit from concentrated prey resources. However, to properly evaluate freshwater pulsing as an energy producer, we must quantify its energetic value, and very few studies have done this, especially for resident species (Stevens et al. 2006). The results of our study provide the first step toward quantifying the potential energetic subsidy of the freshwater pulse to downstream habitats in the form of resident nekton.

### **LITERATURE CITED**

- Alber M (2002) A conceptual model of estuarine freshwater inflow management. *Estuaries* 25:1246-1261
- Arrington DA, Winemiller KO, Layman CA (2005) Community assembly at the patch scale in a species rich tropical river. *Oecologia* 144:157-167
- Barletta M, Barletta-Bergen A, Saint-Paul U, Hubold G (2005) The role of salinity in structuring the fish assemblages in a tropical estuary. *J Fish Biol* 66:45-72
- Barras JA, Beville S, Britsch D, Hartley S, Hawes S, Johnston J, Kemp P, Kinler Q, Martucci A, Porthouse J, Reed D, Roy K, Sapkota S, Suhayda J (2003) Historical and projected coastal Louisiana land changes: 1978-2050. United States Geological Survey Report No. 03-334
- Bretsch K, Allen DM (2006 A) Tidal migrations of nekton in salt marsh intertidal creeks. *Estuaries and Coasts* 29:474-486
- Bretsch K, Allen DM (2006 B) Effects of biotic factors on depth selection by salt marsh nekton. *J Exp Mar Biol Ecol* 334:130-138
- Browder JA, Moore D (1981) A new approach to determining the quantitative relationship between fishery production and flow of fresh water to estuaries. In: Cross R, Williams D

- (eds) Nat Symp on Freshwater Inflow to Estuaries. US Department of the Interior, US Fish and Wildlife Service, Washington D.C., p 403-450
- Castellanos DL, Rozas LP (2001) Nekton use of submerged aquatic vegetation, marsh, and shallow unvegetated bottom in the Atchafalaya River Delta, a Louisiana tidal freshwater ecosystem. *Estuaries* 24:184-197
- Chuang WS, Wiseman WJ Jr (1983) Coastal sea level response to frontal passages on the Louisiana-Texas shelf. *J Geophys Res* 88:2615-2620
- Current CL (1996) Spectral model simulation of wind driven subinertial circulation on the inner Texas-Louisiana shelf waters of the northern Gulf of Mexico. Ph. D.dissertation, Texas A&M University, College Station, TX
- DeAngelis DL, Trexler JC, Loftus WF (2005) Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland. *Can J Fish Aquat Sci* 62:781-790
- Gauch HG, Jr (1982) *Multivariate analysis in community ecology*, Cambridge University Press, Cambridge, MA
- Gillanders BM, Kingsford MJ (2002) Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanogr Mar Biol Annu Rev* 40:233-309
- Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology* 81:2606-2621
- Gotelli NJ, Entsminger GL (2006) *EcoSim: Null models software for ecology*. Version 7. Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT
- Green D, Trexler JC, Lorenz, JJ McIvor CC, Philippi T (2006) Spatial patterns of fish communities along two estuarine gradients in south Florida. *Hydrobiologia* 569:387-399
- Kneib RT (1997) Early life stages of resident nekton in intertidal marshes. *Estuaries* 20:214-230
- Kneib RT (2000) Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Boston, p 267-291
- Kushlan JA (1976) Environmental stability and fish community diversity. *Ecology* 57:821-825
- Lane RR, Day JW, Justic D, Reyes E, Marx B, Day JN, Hyfield E (2004) Changes in stoichiometric Si, N and P ratios of Mississippi River water diverted through coastal wetlands to the Gulf of Mexico. *Est Coast Shelf Sci* 60:1-10
- Loneragan NR, Bunn SE (1999) River flows and estuarine ecosystems: Implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. *Aust J Ecol* 24:431-440

- Montagna PA, Kalke RD (1992) The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries* 15:307-326
- Rozas LP (1995) Hydroperiod and its influence on nekton use of the salt marsh: A pulsing ecosystem. *Estuaries* 18:579-590
- Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20:199-213
- Rozas LP, Odum WE (1987) The role of submerged aquatic vegetation in influencing the abundance of nekton on contiguous tidal fresh-water marshes. *J Exp Mar Biol Ecol* 114:289-300
- Rozas LP, Minello TJ, Munuera-Fernandez I, Fry B, Wissel B (2005) Macrofaunal distributions and habitat change following winter-spring pulsed releases of freshwater into the Breton Sound estuary, Louisiana. *Est Coast Shelf Sci* 65:319-336
- Ruetz CR III, Trexler JC, Jordan F, Loftus WF, Perry, SA (2005) Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance? *J Anim Ecol* 74:322-332
- Ruiz GM, Hines AH, Posey MH (1993) Shallow water as refuge for fish and crustaceans in non-vegetated estuaries. *Mar Ecol Prog Ser* 99:1-16
- Rypel AL, Layman CA, Arrington DA (2007) Water depth modifies relative predation risk for a motile fish taxon in Bahamanian tidal creeks. *Estuaries and Coasts* 30:518-525
- Schaffer WM (1974) Optimal reproductive effort in fluctuating environments. *Am Nat* 108:783-790
- Snedden GA, Cable JE, Swarzenski C, Swenson E (2007 A) Sediment discharge into a subsiding Louisiana deltaic estuary through a Mississippi River diversion. *Est Coast Shelf Sci* 71:181-193
- Snedden GA, Cable JE, Wiseman, WJ (2007 B) Subtidal sea level variability in a Mississippi River deltaic estuary, Louisiana. *Estuaries and Coasts* In Press
- Stevens PW, Montague CL, Sulak KJ (2006) Fate of fish production in a seasonally flooded saltmarsh. *Mar Ecol Prog Ser* 327:267-277
- Stone L, Roberts A (1992) Competitive exclusion, or species aggregation? *Oecologia* 91:419-424
- ter Braak CJF, Smilauer P (2002) CANOCO Reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5), Microcomputer Power, Ithaca, NY

- Thibault RE , Schultz RJ (1978) Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). *Evolution* 32:320-333
- Trexler JC, Loftus WF, Jordan F, Chick JH, Kandl KL, McElroy TC, and Bass, OL, Jr. (2002) Ecological scale and its implications for freshwater fishes in the Florida Everglades. In: Porter JW, Porter KG (eds) *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*. CRC Press, Boca Raton, FL, p 153-180
- Williams AJ, Trexler JC (2006) A preliminary analysis of the correlation of food-web characteristics with hydrology and nutrient gradients in the southern Everglades. *Hydrobiologia* 569:493-504
- Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. *J Fish Biol* 53:267-296

## CHAPTER 4

### USING *GAMBUSIA AFFINIS* GROWTH RATES TO ASSESS ESTUARINE HABITAT QUALITY: A COMPARISON OF INDICES

#### INTRODUCTION

Rapid growth rates have been shown to confer ecological advantage in fishes and reflect favorable conditions such as abundant food, optimal temperatures and appropriate physical habitat (Amara et al. 2007). Indicators of growth and condition provide integrative measures of the effects of both biotic and abiotic environmental influences on fish (Searcy et al. 2007; Zapfe & Rakocinski 2008). As such, these indicators have been used to compare habitat quality (Amara et al. 2007), examine fish response to pollution (Amara et al. 2007) and climatic variability (Teal et al. 2008), inform management of fisheries stocks or endangered species (Lorenzen & Enberg 2002), compare nursery grounds (Gilliers et al. 2004) and assess restored habitats (La Peyre et al. 2007). Over the years, researchers have identified and used several morphometric and biochemical correlates of growth (Table 4.1), however differences in sensitivity and reliability of the methods and the need for species-specific standardization for some methods have hampered efforts to identify appropriate indicators for routine evaluation of habitat quality in the field.

Increasing threats to fish populations, arising from both natural events and anthropogenic activities, have led to extensive estuarine restoration activities around the world and a critical need for appropriate indicators to assess the relationship between restored and altered habitat and their associated fish populations (Madon 2008). In particular, restoration in large-river delta environments (e.g. Williamson River Delta, Sacramento-San Joaquin River Delta, Mississippi

Table 4.1. Commonly used morphometric and biochemical growth indices for fish and key review papers.

Growth/Condition Index	Description	Key Reviews
Morphometric		
Mean length (TL, SL), mean weight	Comparison of fish length or weight over time or in different habitats.	Goede and Barton (1990), Sogard (1992), Ferron and Leggett (1994), Anderson and Neuman (1996), Able (1999), Vila-Gispert and Moreno-Amich (2001), Oliva-Paterna et al. (2003)
Somatic Growth	Rate of change in length (TL,SL) or weight over a set time period.	
Condtion Indices (e.g. Fulton's K, length-weight condition)	Assessment of fish weight at a given length and based on the assumption that heavier fish at a given length have higher relative condition.	
Biochemical		
RNA:DNA	Based on principle that the concentration of cellular DNA remains constant over time while the concentration of RNA changes due to protein synthesis. Higher RNA:DNA correspond to higher protein synthesis and, therefore, somatic growth.	Bulow (1987), Goede and Barton (1990), Ferron and Leggett (1994), Bergeron (1997), Buckley et al. (1999), Caldarone et al. (2006)
Relative DNA content (DNA:DW)	Relatively stable short-term growth index that may show growth differences at the cellular level (hypertrophy vs. hyperplasia) that occur at different ontogenetic stages.	
Gross energy density	Measures the primary energy sources (lipids and protein) in fish tissues by bomb calorimetry, proximate analysis, or predictive empirical models. Higher energy densities correspond to higher energy sources, especially lipids and greater fish condition.	Craig et al. (1978), Flath and Diana (1985), Hartman and Brandt (1995)

River Delta) often focuses on the reconnection of the riverine flood events that provide extended access to high quality, ephemeraally flooded estuarine habitats for transient and resident fishes (Kneib 2000). These flooded habitats have been shown to be functionally valuable for fish growth, due to an abundance of high quality food sources (Madon 2008). In coastal Louisiana, the Caernarvon Freshwater Diversion (Caernarvon) is one such project that restores the annual spring flood pulse to Breton Sound, Louisiana, with the goal of benefiting fish populations. However, managers lack the tools to fully evaluate the impacts of Caernarvon on fish populations or to assess the quality of the downstream habitat in relation to habitat not receiving the restored annual flood pulse.

Numerous measures of growth and condition have been used in both carefully controlled laboratory studies and in a range of field studies (Bergeron 1997; Mercado-Allen et al. 2006; Amara et al. 2007). However, in studies that examine multiple indices on the same fish, low correlations are frequently found between different indices, indicating that the choice of growth and condition indicators of fish may affect conclusions (Gilliers et al. 2004). The lack of correlation between indices has been ascribed to differences in temporal response of the indices, suggesting that the time-scale of the study could be a critical factor influencing the interpretation of results (Gilliers et al. 2004). This difference in temporal response likely results from differences in sensitivity between indices. For example, biochemical indices are often cited as being ideal indicators due to their higher sensitivity and quick detection of growth differences at the cellular level (Rooker et al. 1997; Buckley et al. 1999). However, this high sensitivity may actually decrease the ability of biochemical indices to differentiate habitat quality in field studies, because results can be extremely variable due to numerous factors (i.e. ontogeny, temperature, species), which may ultimately mask differences in habitat quality (Gilliers et al. 2004).



Therefore, it has been suggested that the use of several independent methods may be necessary to minimize problems caused by biases in any one of the methods (Gilliers et al. 2004).

The goals of this study were to 1) evaluate the effects of the restored annual flood pulse and the provision of ephemerally flooded habitat on growth and condition of a ubiquitous marsh resident, the mosquitofish, *Gambusia affinis* and 2) to assess and compare several common morphometric (mean weight, mean length, somatic growth, length-weight condition) and biochemical [RNA:DNA, relative DNA content (DNA:DW), energy density] growth indices. *G. affinis* is an ideal species for this study as it rapidly assembles and uses flooded marsh habitat when available (Kneib 2000; Piazza & La Peyre 2007). To meet these goals, I used a controlled laboratory study, as well as two field experiments that were conducted during a pulsed freshwater release into upper Breton Sound, Louisiana.

### **Study Area**

Breton Sound is a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana (Fig. 4.1). It is microtidal and consists of bays, lakes, bayous, canals, and a relict Mississippi River distributary (Bayou Terre aux Boeufs) that separates the basin geographically and hydrologically. Marshes within the basin consist of fresh, intermediate, brackish, and saline vegetation. This study took place in emergent marshes within the upper Breton Sound basin, which are subject to flooding from Caernarvon. Caernarvon became operational in 1991 and was designed to moderate salinities and reintroduce controlled river inflows to Breton Sound. Yearly winter/spring experimental high-flow releases began in spring 2001 to simulate seasonal flood-pulse events and mimic springtime flooding conditions that are experienced in river dominated Gulf Coast estuaries (Rozas 1995). Pulses release periodic large fluxes of Mississippi river water into the basin, and are capable of inundating upper basin marshes (inflow marshes; ~ 5,700 ha) for extended periods (Snedden et al. 2007).

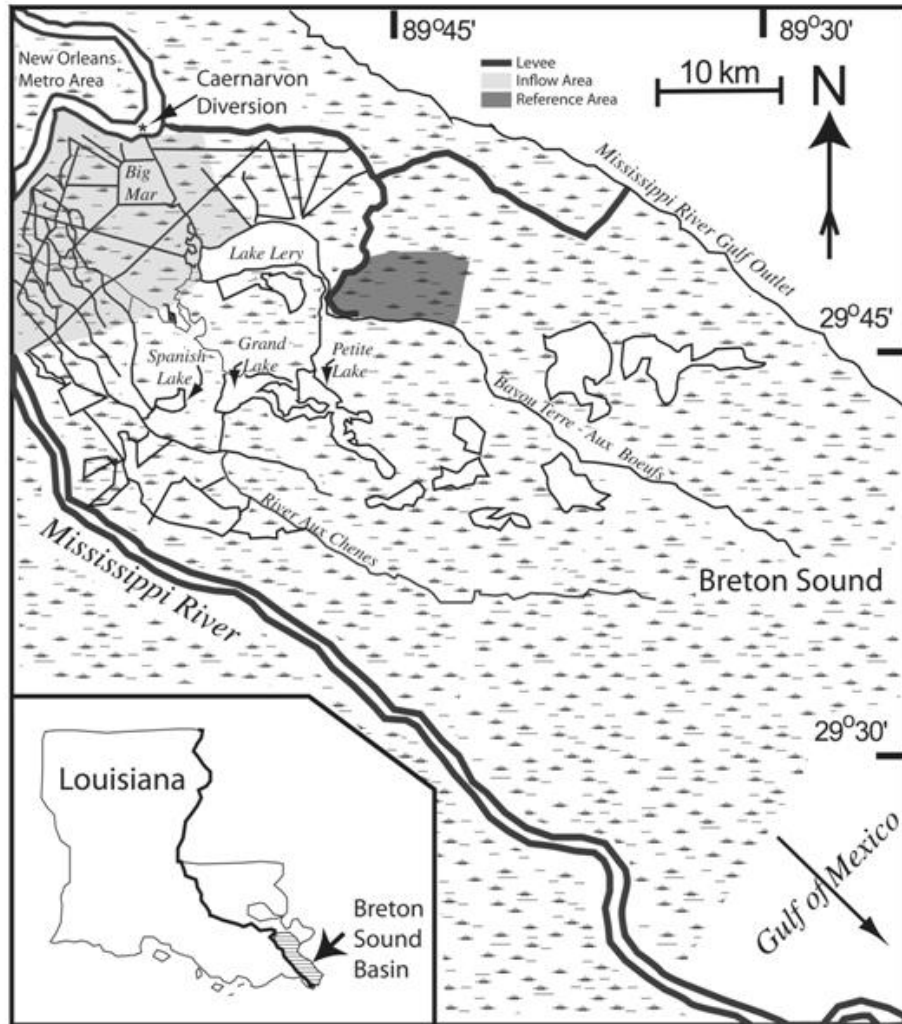


Fig. 4.1. Map showing Breton Sound estuary, Louisiana and the location of the Caernarvon Freshwater Diversion. Shaded areas show the location of the inflow (light gray) and reference (dark gray) areas used in this study. Map taken from Piazza & La Peyre (2007).

In 2007, one sustained high-discharge event was conducted (January – March). Like other Gulf Coast estuaries, without the riverine pulse, inundation of upper basin marshes is dominated by meteorological forcing (Rozas 1995). These conditions are found in the marshes east of Bayou Terre Aux Boeufs, which are hydrologically separated from diversion flow, creating a reference area (reference marshes; Rozas et al. 2005). Dominant emergent vegetation in both inflow and reference marshes consists of *Spartina patens* (Saltmeadow cordgrass) and *Schoenoplectus americanus* (Chairmaker's bulrush).

## **METHODS**

### **Laboratory Experiment 1: Precision of Nucleic Acid Purification Technique**

The goal of this experiment was to test the precision of the Qiagen AllPrep DNA/RNA Mini Kit (Qiagen, Inc.) for nucleic acid purification and quantification.

#### **Experimental Design**

Ten wild *G. affinis* were randomly collected from Breton Sound, LA (outside of both inflow and reference areas) with a dip net. Upon capture, fish were placed in an aerated holding tank and transported alive back to Louisiana State University for processing. Experimental fish were weighed (g) and measured [total length (TL), standard length (SL), mm], and a single piece of white muscle tissue (~ 30 mg) was dissected from the side of each fish for nucleic acid extraction. Tissue samples from each fish were homogenized under liquid nitrogen and separated into three subsamples. Nucleic acids were purified and measured and RNA:DNA was calculated for each subsample, following protocols below.

#### **Data Analysis**

Precision of the nucleic acid purification and quantification technique was determined with a univariate ANOVA that compared RNA:DNA of individual fish. Additionally, the coefficient of variation [CV; (standard deviation / mean)\*100] was used as the measure of the precision of the overall technique (purification and quantification; Caldarone et al. 2006).

### **Laboratory Experiment 2: Growth Experiment**

The goals of this experiment were to 1) standardize techniques of measuring growth and condition for wild *G. affinis*, and 2) compare common growth indices (somatic growth, length-weight condition, RNA:DNA, relative DNA content) on the same wild fish under controlled laboratory conditions. The experiment was necessary because there are few studies that investigate growth of *G. affinis* and none that calculated RNA:DNA or relative DNA content for

this species, and nucleic acid concentrations vary widely across fish species (Pederson 1971).

Additionally, few studies use wild fish for RNA/DNA experimentation, but rather use lab-reared cohorts under strict control.

### Experimental Setup and Design

Experimental fish were harvested with dip nets in upper Breton Sound estuary (outside of both inflow and reference areas) during July 2006. Upon capture, fish were placed in an aerated holding tank and immediately treated with *Furanace* freshwater and marine environmental control for bacterial infections (Aquarium Products, Inc., Glen Burnie, MD) at a rate of 2 tablets per 38 l to combat fatal outbreaks of *Columnaris* spp. bacteria which are endemic to wild fish in coastal Louisiana (John Hawke, Dept. of Pathobiological Sciences, LSU School of Veterinary Medicine, personal communication). Captured fish were transported back to LSU and acclimated for two weeks in three separate holding tanks (142 l) during which time *Furanace* was continually applied (2 tablets per 38 l per day for two days, one tablet per 38 l per day thereafter). During the acclimation period, all fish were fed commercial fish food (Omega One flake fish food, Omega Sea, Ltd, Sitka, AK) once daily.

Twenty experimental aquaria (76 l) were set up one month prior to experimental initiation and identically equipped with undergravel filtration and a common air source (Coralife Super Luft Pump, SL-65, high-pressure aquarium air pump; output pressure - 3.9 psi, output flow rate –  $2.3 \text{ ft}^3 \text{ min}^{-1}$ ,  $65 \text{ l min}^{-1}$ ). AquaSafe water conditioner (Tetra Aqua, Inc., Blacksburg, VA) was used for water dechlorination, at a rate of 5 ml per 38 l. Water temperature in the experimental aquaria was kept at ambient temperature (18-19° C), and the light/dark cycle was 12 hr throughout the experiment.

Each aquarium was randomly assigned to one of two treatments (fed or starved), and these laboratory treatments served as a proxy for habitat quality. Starved fish were not fed

throughout the 10 day experiment. Fed fish were provided commercial fish food (Omega One flake fish food, Omega Sea, Ltd, Sitka, AK) *ad libitum* every six hours (08:00, 14:00, 20:00, 02:00) until they did not actively strike food for one minute and left some food floating on the surface.

Thirty-three experimental fish were randomly chosen, stocked to each aquarium (Total N = 660) and acclimated (unfed) for one day. At the end of the acclimation period and before the initial feeding, three fish were removed from each tank and processed for initial condition measurement (Day 0). Three fish were then removed from each tank daily (07:00) for somatic growth and tissue analysis (3 fish x 20 tanks = 60 fish d<sup>-1</sup>) for a total of 11 days (220 tank means). Upon removal, fish were weighed (g), measured (mm) and a piece of white muscle tissue (~ 30 mg) was dissected from the side of each fish for nucleic acid extraction and calculation of nucleic acid indices.

#### Data Analysis

Wet weights of experimental fish were converted to dry weights by using a species-specific regression equation for *G. affinis* (Piazza & La Peyre, In Review):

$$DW = -0.002934 + 0.206633(WW)$$

Daily somatic growth (g DW, mm) for each treatment was determined by regression analysis (model growth = day; SAS PROC REG) on a daily tank mean of harvested fish (n = 3 fish tank<sup>-1</sup> d<sup>-1</sup>). Linear regression was also used to investigate daily trends in RNA:DNA, and relative DNA content. All results were considered significant at  $\alpha = 0.05$ .

Correlation analysis was used to investigate the relationship between morphometric growth indices, individual nucleic acid concentrations, RNA:DNA, and relative DNA content. The CV was calculated as an overall measure of variability of the individual nucleic acid measurements, RNA:DNA, and relative DNA content (Weber et al. 2003).

## Field Experiment 1: Enclosure Growth Experiment

This 10 d field experiment involved the measurement of growth on wild-caught *G. affinis* that were placed in enclosures in the field. The goal was to examine the response of multiple growth indices (somatic growth, length-weight condition, RNA:DNA, and relative DNA content) as indicators of short-term response to restored freshwater inflow.

### Experimental Setup and Design

In spring 2007, during the freshwater release, wild *G. affinis* were caught with dip nets in upper Breton Sound estuary (outside both inflow and reference areas) and acclimated for 24 h. Eight enclosures (208 l) were placed in each treatment area during a high-flow pulse event and stocked at a density (5 fish enclosure<sup>-1</sup>) that reflected the ambient density of *G. affinis* in flooded marshes during 2005 and 2006 winter/spring pulse releases (Piazza & La Peyre 2007). Enclosures were deployed six weeks after the pulse event began to account for any lagged system responses that may result during pulsed freshwater releases. At the time of deployment, water temperature (°C), conductivity (ms), salinity (psu), and dissolved oxygen (mg l<sup>-1</sup>) were measured with a handheld YSI 556 MPS (YSI Environmental, Inc.). Turbidity (NTU) was measured with a fluorometer (Aquaflour 8000, Turner Designs, Inc.).

Each experimental fish was uniquely marked for identification and was measured (TL, SL, weight) upon deployment and retrieval, 10 days later. Additionally upon retrieval, a random sample of three fish from each enclosure was chosen for RNA/DNA analysis, and a piece of white muscle tissue (~ 30 mg) was dissected from the side of each fish for nucleic acid extraction.

### Data Analysis

Wet weights of experimental fish were converted to dry weights, and daily somatic growth (Gw) was calculated by using the equation

$$G_w (\text{g DW d}^{-1}) = (\ln DW_{t2} - \ln DW_{t1})/10 \text{ d}$$

Univariate ANOVA was used to investigate treatment differences in somatic growth, RNA:DNA and relative DNA content (response variable = treatment).

### **Field Experiment 2: Through-Pulse Field Collection Experiment**

This experiment involved discrete collection and measurement of growth indices for wild *G. affinis* weekly through the pulse event. The goal was to examine the response of multiple growth indices (somatic growth, RNA:DNA, relative DNA content, length-weight condition, energy density) as indicators of longer-term temporal response to freshwater input.

#### Experimental Design

I collected wild *G. affinis* with a dip net at several randomly chosen sites across flooded inflow and reference marshes through the experimental flood pulse event. Collections began on the first day of the pulse release and were made weekly for seven weeks (January 6 – March 12), resulting in a total of 2,038 wild *G. affinis*. Environmental variables were measured (as above) each week at the time of fish collection.

Immediately upon capture, each fish was weighed (g) and measured (TL, mm) and randomly divided into two groups. One group ( $n=15$  fish week<sup>-1</sup> from each treatment area) was randomly selected from the total fish pool for RNA/DNA analysis, and a piece of white muscle tissue (~ 30 mg) was immediately dissected from the side of each fish for nucleic acid extraction. This group ( $N = 210$  fish) provided comparison of morphometric growth indices and nucleic acid indices (RNA:DNA and relative DNA content). The second group (comprised of the remaining fish;  $N = 1,828$  fish) was used for analyses of length-weight condition and energy density. These fish were immediately frozen in an ice slurry and transported back to the laboratory where they were measured (length mm, WW g) for length-weight condition analysis and processed for energy density analysis.

## Data Analysis

Wet weights of experimental fish were converted to dry weights, and weekly growth was determined for each treatment by regression analysis (model growth = week) performed on a weekly sample mean of collected fish. Linear regression was also used to investigate weekly trends in RNA:DNA, relative DNA content, and energy density.

Correlation analysis was used to investigate the relationship between morphometric growth indices, individual nucleic acid concentrations, RNA:DNA, and relative DNA. The CV was calculated as an overall measure of variability of the individual nucleic acid measurements, RNA:DNA, and relative DNA content (Weber et al. 2003).

## **Experimental Protocols**

### Nucleic Acid Indices

Immediately upon harvest, a single piece of white muscle tissue (~ 30 mg) was dissected from the side of each fish for nucleic acid extraction. Each sample was weighed, immediately transferred to sterilized, RNase/DNase free microcentrifuge tubes filled with 400 ul *RNAlater* (Qiagen Inc.), refrigerated overnight, and stored (-80°C). Each tissue sample was removed from the freezer, thawed, disrupted to a powder in a mortar and pestle under liquid nitrogen, and homogenized in a QIAshredder spin column (Qiagen, Inc.) under a buffer. RNA and DNA purification was performed simultaneously with the AllPrep DNA/RNA Mini Kit (Qiagen, Inc; [www.qiagen.com](http://www.qiagen.com)). This kit allowed the parallel purification of both cellular RNA and DNA from the same tissue sample.

Once purified, concentrations of both RNA (ng/uL) and DNA (ng/uL) were measured with nucleic acid-specific dye assays in a 96-well plate format. RNA concentrations were measured with the Quant-IT RiboGreen RNA Kit (Item R11490, Molecular Probes, Invitrogen, Inc.). Concentrations of DNA were measured with the Quant-IT dsDNA Broad-Range Assay



Kit (Item MP3310, Molecular Probes, Invitrogen, Inc.). Duplicate repetitions of each assay (RNA and DNA) were performed for all samples.

Fluorescence measurements were made on a Cytofluor II multi-well fluorescence plate reader (PerSeptive Biosystems, Framingham MA), set at 480/535 nm (excitation/emission) for both RNA and DNA measurements. Fluorescence values (nm) for samples were converted to concentrations with the standard curves. DNA standard curves were constructed with eight different concentrations of dsDNA (0, 5, 10, 20, 40, 60, 80, 100 ng/uL; Quant-IT dsDNA Broad-Range Assay Kit). RNA standard curves were constructed with five dilutions of 16s and 23s rRNA from *Escherichia coli* (0, 1, 5, 25, 50 ng/mL; Quant-IT RiboGreen RNA Kit). RNA and DNA concentrations were standardized to 1 mg of tissue weight ( $\mu\text{g}/\text{mg}$ ), and RNA:DNA was expressed as the ratio of concentrations.

The relative DNA content was expressed as the ratio of the DNA concentration from an individual experimental fish to the dry weight of that fish (DNA:DW). This ratio has been recommended for further study as a reliable nucleic acid-based indicator of short-term growth (Bergeron 1997, Buckley et al. 1999).

#### Length-Weight Condition

Fish condition was determined with the approach used by Vila-Gispert and Moreno-Amich (2001) and Oliva-Paterna et al. (2003). A univariate analysis of covariance (ANCOVA) was conducted on weight (dependent variable) and length (covariate) variables, which were each log-transformed to ensure linearity. Homogeneity of slopes of dependent-covariate relationships was tested with an ANCOVA model design that included the pooled covariate-factor interaction. In cases where the slopes were homogeneous, a standard ANCOVA was used to test for differences between treatments at the y-intercept. In cases where the slopes were heterogeneous, the mean weights were tested for equality at the overall mean of the covariate.

### Energy Density

Experimental fish were dried to a constant weight (50° C, 48 h), weighed (g DW), and pulverized using a combination of mortar and pestle and a hand-held electric coffee grinder. Analysis of energy density (cal g<sup>-1</sup>) was done on one gram (DW) nekton pellets (Parr model 2811 pellet press) with a Parr 6200 isoperibol oxygen bomb calorimeter (oxygen bomb model 1108). Each pellet represented numerous individuals collected in a specific sample, and the number was dependent on the size of the individuals caught. Enough experimental *G. affinis* were captured to yield a total of N = 36 pellets (22 inflow, 14 reference) for calorimetry analysis. This subset of experimental fish was used to compare energy density and length-weight condition.

## **RESULTS**

### **Laboratory Experiment 1: Precision of Nucleic Acid Purification Technique**

The overall mean (SE) RNA:DNA of *G. affinis* used to test the precision of the Qiagen AllPrep DNA/RNA Mini Kit was 8.66 (0.64). ANOVA results showed no significant difference in RNA:DNA among tissue subsamples taken from each fish ( $F_{2, 18} = 1.47$ ;  $p = 0.25$ ;  $N = 60$ ). The precision of the technique as measured by the CV was 12%.

### **Laboratory Experiment 2: Growth Experiment**

#### Fish Recovery

A total of 610 fish were recovered, with 50 (8%) deaths during the experiment. Fish death began after 5 days, and occurred evenly in starved (50%) and fed (50%) tanks. Nucleic acids were successfully extracted from 545 experimental fish (515 female, 30 male), approximately evenly split between adults (55%) and juveniles (45%). Somatic and nucleic acid growth indices were calculated from 207 tank means.

#### Fish Growth

Mean ( $\pm$  SE) weight and length of experimental *G. affinis* was  $0.14 \pm 0.00$  g WW ( $0.02 \pm 0.00$  g DW) and  $23.01 \pm 0.18$  mm TL, respectively. Regression analysis showed significant

daily somatic growth of fish from the fed treatment for both weight [Weight (g DW) = 0.001 (day) + 0.026;  $r^2 = 0.05$ ;  $p = 0.02$ ;  $N = 104$ ] and total length [Length (mm) = 0.19 (day) + 22.61;  $r^2 = 0.05$ ;  $p = 0.02$ ;  $N = 104$ ]. Starved fish showed zero daily growth in weight or length.

#### Nucleic Acid Indices:

RNA:DNA ratios and relative DNA content were highly variable throughout the experiment (Table 4.2). Nucleic acid concentrations were correlated with each other and RNA:DNA (Table 4.3). Regression analysis showed significant daily increases for RNA:DNA for both fed fish [RNA:DNA = 0.82 (day) + 0.62;  $r^2 = 0.30$ ;  $p < 0.0001$ ;  $N = 104$ ] and starved fish [RNA:DNA = 0.34 (day) + 3.93;  $r^2 = 0.09$ ;  $p = 0.003$ ;  $N = 103$ ], with a greater increase in fed fish as compared to starved fish. Relative DNA content showed significant daily decrease in fed fish [DNA:DW = - 0.0002 (day) + 0.03;  $r^2 = 0.11$ ;  $p = 0.0004$ ;  $N = 104$ ] and no significant daily relationship for starved fish.

#### Length-Weight Condition

Fish condition across all days (Fig. 4.2) was tested at the overall mean weight (0.82 g WW) due to heterogeneity of slopes. Length-weight condition was significantly greater (ANCOVA  $p < 0.0001$ ,  $N = 610$ ) in fed fish ( $y = 3.0096x + 2.3841$ ;  $r^2 = 0.88$ ) than starved fish ( $y = 2.7522x + 2.4228$ ;  $r^2 = 0.82$ ). Analysis of length-weight condition by day showed no difference in the condition of fish by treatment at Day 0 (initial condition) and significantly greater condition for fed fish each day thereafter (Days 1 – 10).

#### Comparison of Techniques

RNA and DNA concentrations, as well as relative DNA content were significantly negatively correlated with mean weight, but RNA:DNA was not significantly correlated with mean weight (Table 4.3). These patterns held even when analyzed by treatment, for fed and starved fish. RNA:DNA, length-weight condition and mean weight all showed greater positive

Table 4.2. Lab experiment 2: Growth experiment. Summary statistics by treatment for cellular RNA and DNA concentrations and nucleic acid growth indices. Nucleic acids were purified from wild *Gambusia affinis* caught in upper Breton Sound, Louisiana during summer 2007 and used in the 10-day laboratory feeding experiment. Means are based on N = 207 tank means.

Laboratory Experiment				
Growth/Condition Index	Fed Treatment (N = 104)		Starved Treatment (N = 103)	
	Mean $\pm$ SE (Range)	CV (%)	Mean $\pm$ SE (Range)	CV (%)
RNA ( $\mu\text{g mg}^{-1}$ )	1.95 $\pm$ 0.17 (0.23 - 11.59)	91	3.31 $\pm$ 0.22 (0.10 - 13.15)	66
DNA ( $\mu\text{g mg}^{-1}$ )	0.52 $\pm$ 0.03 (0.14 - 2.06)	55	0.63 $\pm$ 0.03 (0.19 - 1.95)	48
RNA:DNA	4.51 $\pm$ 0.44 (0.56 - 31.47)	101	5.53 $\pm$ 0.35 (0.34 - 19.31)	64
DNA:DW	0.02 $\pm$ 0.00 (0.00 - 0.16)	98	0.04 $\pm$ 0.00 (0.00 - 0.43)	119

changes in fed fish during the experiment, although the increase in RNA:DNA lagged the response of condition and somatic growth by approximately 7 days (Fig 4.2).

### Field Experiment 1: Enclosure Growth Experiment

#### Environmental Characteristics

Environmental characteristics were typical of upper Breton Sound in early spring (Lane et al. 2007, Table 4.4). No treatment difference was found for water temperature, salinity or dissolved oxygen, and daily fluctuations occurred in unison within and across treatments.

Turbidity was higher in inflow marshes, and mean water depth was approximately 10 cm greater in reference marshes.

Table 4.3. Lab experiment 2: Growth experiment. Pearson product moment correlation results for nucleic acid-based growth indices and somatic daily growth during a 10-day laboratory experiment with wild *Gambusia affinis*. All correlations are based on N = 207 daily tank means. Fish weight and total length were significantly correlated; therefore only correlations with weight are reported. P-values are located within parentheses, and bold type signifies statistical significance at  $\alpha = 0.05$ .

Variable	DNA	RNA:DNA	DNA:DW	Mean Weight (g DW)
RNA ( $\mu\text{g mg}^{-1}$ )	0.44 (< <b>0.0001</b> )	0.72 (< <b>0.0001</b> )	0.54 (< <b>0.0001</b> )	-0.32 ( <b>0.007</b> )
DNA ( $\mu\text{g mg}^{-1}$ )		-0.16 ( < <b>0.02</b> )	0.79 (< <b>0.0001</b> )	-0.43 ( <b>0.0001</b> )
RNA:DNA			-0.02 (0.75)	0.02 (0.77)
DNA:DW				-0.52 (< <b>0.0001</b> )

### Fish Recovery

Overall, 37 fish were recovered, and 43 (53%) fish were not recovered during the experiment. Fish recovery was lowest in the reference area (11 fish from 3 sites), due to the high variability in water levels and the potential for marsh drying. Fish were recovered from 3 sites in the reference area and all four sites in the inflow area.

### Fish Growth

Initial mean weight and length of experimental *G. affinis* was  $0.33 \pm 0.02$  g WW ( $0.07 \pm 0.00$  g DW) and  $31.51 \pm 0.54$  mm TL, respectively. Overall mean daily somatic growth of fish in the inflow area was significantly higher than the reference area ( $F_{1,35} = 13.22$ ;  $p=0.0009$ ; Fig. 4.3). In the inflow area, the highest mean weight gain occurred at the site closest to the diversion structure, where the gain was double ( $0.001$  g DW  $\text{d}^{-1}$ ) the overall mean daily weight gain observed in the inflow area (Table 4.5). Interestingly, this growth rate matched the daily growth rate for fed fish in the laboratory experiment.

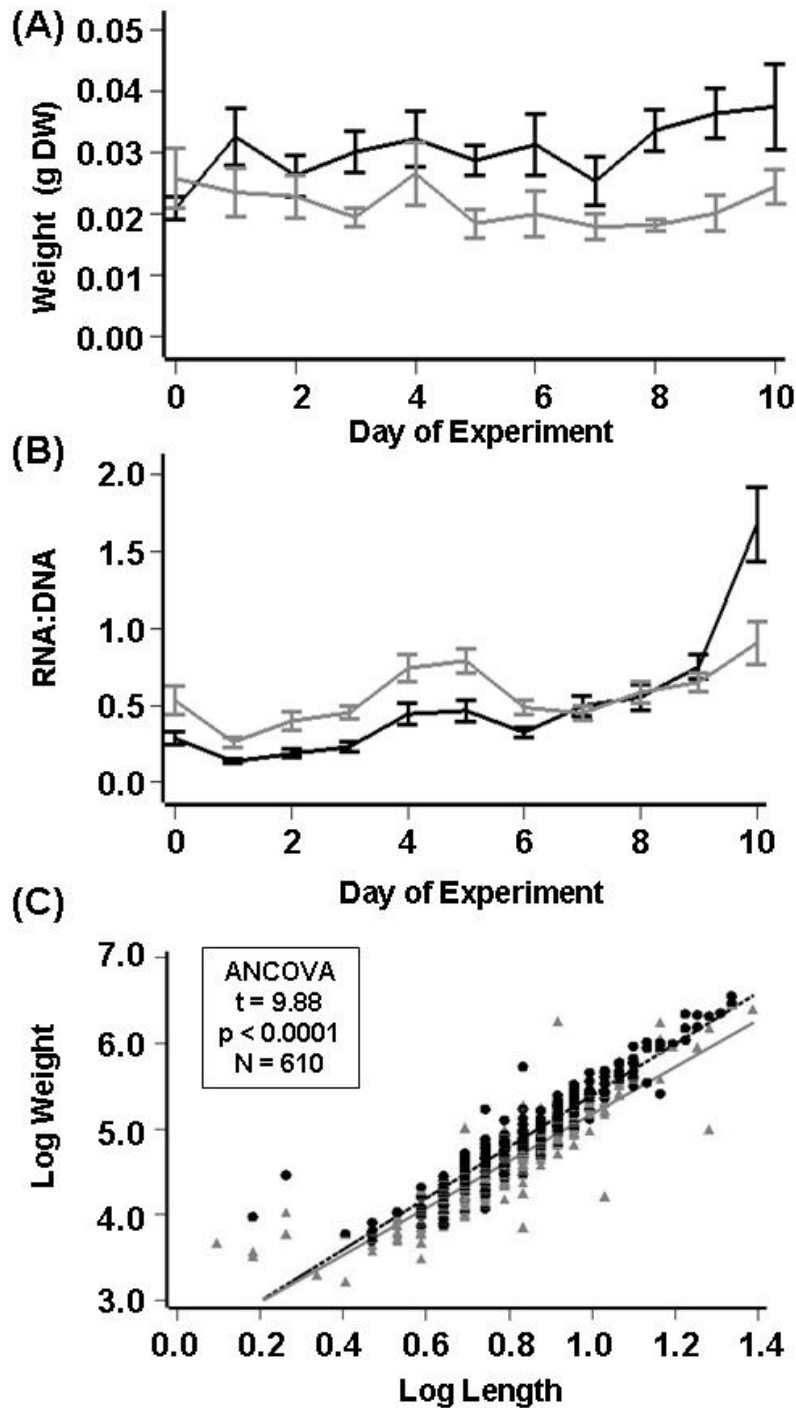


Fig. 4.2. Lab experiment 2: Growth experiment. Comparison of (A) daily mean weight (g DW), (B) RNA:DNA, and (C) length-weight condition for wild-caught *Gambusia affinis* through a 10-day laboratory growth experiment. Fish in the fed treatment were fed a commercial flake food *ad-libitum* every six hours for 10 days. Fish in the starved treatment were withheld food during the 10 day period. Comparisons of growth rate and RNA:DNA are based on  $N = 207$  tank means. Length-weight condition is based on  $N = 610$  fish. In all graphs, black represents fed fish, and gray represents starved fish.

### Nucleic Acid Indices

Mean RNA:DNA of fish in the inflow area was greater than that in the reference area, however this relationship was not significant at  $\alpha = 0.05$  (Fig.4.3). Relative DNA content was also similar between treatments (Table 4.5).

### Length-Weight Condition

Due to heterogeneity of slopes, condition of harvested fish (Fig. 4.3) was tested at the overall mean weight (1.15 g WW). Length-weight condition was similar in inflow ( $y = 3.3531x + 1.9283$ ;  $r^2 = 0.95$ ) and reference ( $y = 3.1252x + 2.1440$ ;  $r^2 = 0.86$ ) fish.

### Comparison of Techniques

A statistical difference was found only for somatic growth in this study; however length-weight condition, RNA:DNA both showed the similar trend of greater positive responses in inflow fish (Fig. 4.3). Relative DNA content did not show a pattern that would suggest greater growth in inflow fish.

## **Field Experiment 2: Through-Pulse Field Collection Experiment**

### Environmental Characteristics

Environmental characteristics during the field collection were typical of upper Breton Sound throughout the study period (Lane et al. 2007, Table 4.4). No difference was found for water temperature or dissolved oxygen by treatment or week. Variation in environmental characteristics occurred across all sites and both treatments simultaneously. Turbidity was higher in inflow marshes, while water depth and salinity were slightly greater in reference marshes.

Nucleic acids were successfully extracted and compared to somatic growth for 208 experimental fish (104 inflow, 104 reference). Experimental fish were mostly composed of adults (95%) and females (90%). Analyses of length-weight condition and energy density

Table 4.4. Field experiment 1 and 2: Environmental characteristics of upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. The enclosure experiment, began at week six of the pulse and lasted 10 days. The field collection experiment began on the first day of the pulse event and lasted seven weeks.

Variable	Enclosure Experiment N = 40		Field Collection Experiment N = 6	
	Inflow	Reference	Inflow	Reference
	Mean $\pm$ SE (Range)	Mean $\pm$ SE (Range)	Mean $\pm$ SE (Range)	Mean $\pm$ SE (Range)
Temperature ( $^{\circ}$ C)	15.7 $\pm$ 0.4 (13.5 - 20.5)	15.8 $\pm$ 0.20 (14.5 - 17.6)	13.4 $\pm$ 1.46 (7.2 - 16.1)	14.3 $\pm$ 2.31 (6.2 - 22.3)
Salinity (psu)	0.2 $\pm$ 0.00 (0.2 - 0.2)	0.9 $\pm$ 0.12 (0.23 - 2.08)	0.2 $\pm$ 0.01 (0.2 - 0.2)	2.1 $\pm$ 0.17 (1.7 - 2.7)
Dissolved Oxygen ( $\text{mg l}^{-1}$ )	8.4 $\pm$ 0.13 (6.6 - 9.3)	8.1 $\pm$ 0.09 (7.3 - 8.7)	5.9 $\pm$ 0.88 (3.6 - 8.4)	4.7 $\pm$ 0.81 (2.2 - 7.6)
Turbidity (NTU)	18.6 $\pm$ 3.09 (1.6 - 53.0)	8.4 $\pm$ 1.06 (1.1 - 19.5)	13.0 $\pm$ 2.28 (5.5 - 18.6)	4.4 $\pm$ 1.24 (2.1 - 10.4)
Water Depth (mm)	201.8 $\pm$ 10.46 (122.4 - 314.2)	330.4 $\pm$ 9.15 (223.6 - 400.4)	173.2 $\pm$ 15.7 (125.0 - 215.0)	275.0 $\pm$ 65.82 (150.0 - 510.0)

was performed on 1,828 experimental fish, although they were transformed into N = 36 one-gram pellets (22 inflow, 14 reference) for energy density analysis.

### Fish Growth

Overall mean ( $\pm$  SE) weight and length of experimental *G. affinis* was 0.24  $\pm$  0.01 g WW (0.05  $\pm$  0.00 g DW) and 28.35  $\pm$  0.27 mm TL, respectively. Regression analysis showed no significant weekly growth pattern in weight or length from fish caught in the inflow area. A significant negative weekly relationship existed for both fish weight [Weight (g DW) = - 0.007 (week) + 0.076;  $r^2$  = 0.34;  $p$  < 0.0001; N = 104] and total length [Length (mm) = - 1.41 (week) + 34.06;  $r^2$  = 0.41;  $p$  < 0.0001; N = 104] in the reference area.



### Nucleic Acid Indices

RNA:DNA and relative DNA content were highly variable throughout the experiment (Table 4.6). Nucleic acid concentrations correlated positively with each other, and RNA:DNA correlated positively with RNA concentrations and negatively with DNA concentrations (Table 4.7). Regression analysis showed a significant weekly increase in RNA:DNA for both inflow fish [RNA:DNA = 2.28 (week) - 2.98;  $r^2 = 0.30$ ;  $p < 0.0001$ ;  $N = 104$ ] and reference fish [RNA:DNA = 1.60 (week) + 0.68;  $r^2 = 0.24$ ;  $p < 0.0001$ ;  $N = 104$ ], with a greater increase in inflow fish than reference fish. Relative DNA content showed no weekly relationship in inflow fish and a significant positive weekly relationship in reference fish [DNA:DW = 0.003 (week) + 0.005;  $r^2 = 0.10$ ;  $p = 0.0008$ ;  $N = 104$ ].

### Length-Weight Condition

Condition of harvested fish (Fig. 4.4) was tested at the y intercept, because slopes were homogeneous. Overall length-weight condition was significantly higher in reference fish ( $y = 2.8140x - 4.2528$ ;  $r^2 = 0.89$ ;  $N = 1044$ ) than inflow fish ( $y = 2.8908x - 4.3808$ ;  $r^2 = 0.91$ ;  $N = 784$ ). Analysis by week showed that in the first four weeks, the index was higher for reference fish for three weeks (weeks 2, 3, 4). At week five, the index showed no difference in value between treatments, and this pattern remained constant through weeks six and seven.

### Energy Density

Overall mean energy density of experimental *G. affinis* during the 2007 freshwater pulse event was  $6,242 \pm 40.79$  cal g<sup>-1</sup> (range 4,863 – 6,719 cal g<sup>-1</sup>). Regression analysis showed a significant weekly increase in energy density for inflow fish [Energy (cal g<sup>-1</sup>) = 80.08 (week) + 5855.09;  $r^2 = 0.28$ ;  $p < 0.01$ ;  $N = 22$ ]. No weekly relationship was found for reference fish. The largest increase in energy density occurred in the inflow samples, and was observed during weeks 1 – 3, with a second, but smaller increase observed between weeks six and seven.

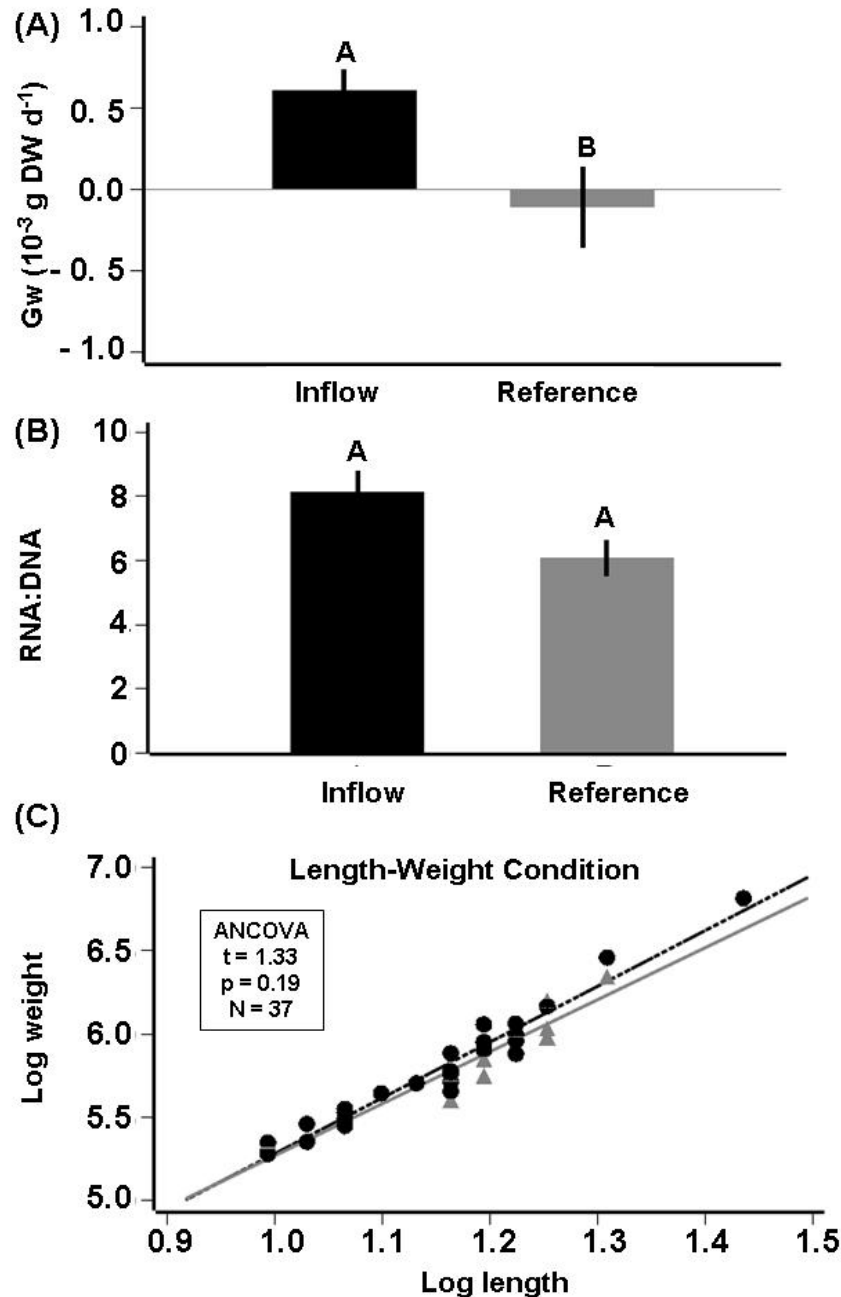


Fig. 4.3. Field experiment 1: Enclosure growth. Comparison of (A) daily growth (g DW d<sup>-1</sup>) index, (B) RNA:DNA, and (C) length-weight condition for wild-caught *Gambusia affinis* through a 10-day field enclosure growth experiment in upper Breton Sound, Louisiana. Inflow fish were contained in enclosures in flooded marsh habitat for 10 days beginning at week six of an extended freshwater pulse event downstream from the Caernarvon Freshwater Diversion. Reference fish were contained in flooded marsh habitat unaffected by the freshwater pulse. Comparisons of growth rate, RNA:DNA, and length-weight condition are based on N = 37 experimental fish (26 inflow, 11 reference) recaptured in enclosures after the 10-day experiment. In all graphs, black represents inflow fish, and gray represents reference fish.

Table 4.5. Field experiment 1: Enclosure experiment. Summary statistics by treatment for morphometric and nucleic acid growth indices for wild *Gambusia affinis* during a short-term enclosure growth experiment in upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. The enclosure experiment, began at week six of the pulse and lasted 10 days. The rate of change in TL is reported, as opposed to SL, in order to remain consistent across experiments. The change in SL was also measured and the results are the same as TL.

Enclosure Experiment					
Growth/Condition Index	Inflow Area (N = 26)		Reference Area (N = 11)		ANOVA Results
	Mean $\pm$ SE (Range)	CV (%)	Mean $\pm$ SE (Range)	CV (%)	Trt
					<u>F-value</u>
Weight (g DW d <sup>-1</sup> )	0.0006 $\pm$ 0.00 (-0.0004 - 0.003)	-	-0.0001 $\pm$ 0.00 (-0.001 - 0.002)	-	13.36**
Total Length (mm d <sup>-1</sup> ) <sup>1</sup>	0.08 $\pm$ 0.01 (0.00 - 0.20)	-	0.009 $\pm$ 0.01 (0.00 - 0.10)	-	15.53**
RNA ( $\mu$ g mg <sup>-1</sup> )	3.46 $\pm$ 0.42 (0.63 - 7.89)	48	2.73 $\pm$ 0.51 (0.38 - 5.45)	62	1.20
DNA ( $\mu$ g mg <sup>-1</sup> )	0.44 $\pm$ 0.05 (0.14 - 0.87)	42	0.42 $\pm$ 0.04 (0.24 - 0.69)	35	0.05
RNA:DNA	8.16 $\pm$ 0.86 (4.29 - 15.19)	41	6.07 $\pm$ 0.80 (0.92 - 9.90)	44	2.94
DNA:DW	0.01 $\pm$ 0.00 (0.00 - 0.02)	63	0.01 $\pm$ 0.00 (0.00 - 0.02)	62	0.32

<sup>1</sup> The rate of change in TL is reported to remain consistent across experiments. The change in SL was also measured and results were similar.

### Comparison of Techniques

General patterns of change were similar between indices (Fig. 4.4). Values for mean weight, somatic growth, RNA:DNA, energy density, and length-weight and condition were initially lower in inflow fish, but over the course of the experiment, inflow fish showed a greater increase

Table 4.6. Field experiment 2: Through-pulse field collection. Summary statistics by treatment for nucleic acid growth indices for wild *Gambusia affinis* during a through-pulse field collection experiment in upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. The field collection experiment began on the first day of the pulse event and lasted seven weeks.

Field Collection Experiment				
Growth/Condition Index	Inflow Area (N=104)		Reference Area (N=104)	
	Mean $\pm$ SE (Range)	CV (%)	Mean $\pm$ SE (Range)	CV (%)
RNA ( $\mu\text{g mg}^{-1}$ )	2.54 $\pm$ 0.18 (0.01 - 15.24)	104	3.24 $\pm$ 0.18 (0.30 - 15.31)	83
DNA ( $\mu\text{g mg}^{-1}$ )	0.51 $\pm$ 0.02 (0.08 - 1.34)	45	0.51 $\pm$ 0.02 (0.14 - 1.63)	51
RNA:DNA	6.21 $\pm$ 0.58 (0.03 - 46.63)	134	7.15 $\pm$ 0.45 (1.20 - 38.63)	92
DNA:DW	0.01 $\pm$ 0.00 (0.00 - 0.04)	70	0.02 $\pm$ 0.00 (0.00 - 0.10)	112

and higher final values. Differences were detected in the timing of increase among indices. In particular, while morphometric and energy density indices all responded within the first 4 - 5 weeks of the pulse event, RNA:DNA response lagged the response of these indices by approximately one week (Fig. 4.4). This one-week lag in RNA:DNA response is consistent with that observed in the laboratory experiment. Correlations between biochemical indices followed a similar trend to that found in the lab experiment (Table 4.7).

Table 4.7. Field experiment 2: Through-pulse field collection. Pearson product moment correlation results for nucleic acid-based growth indices and mean weight (g DW) of wild-caught *Gambusia affinis* in upper Breton Sound estuary, Louisiana during an extended winter-spring riverine pulse event beginning January 26, 2007. Field collections began on the first day of the pulse event and lasted seven weeks. Correlations for all indices except energy density are based on N = 208 fish. Comparisons with energy density are based on N = 36 one-gram DW pellets, composed of 1,828 fish. Fish weight and total length were significantly correlated; therefore only correlations with weight are reported. P-values are located within parentheses, and bold type signifies statistical significance at  $\alpha = 0.05$ .

Variable	DNA	RNA:DNA	DNA:DW	Energy (cal g <sup>-1</sup> )	Weight (g DW)
RNA (µg mg <sup>-1</sup> )	0.16 ( <b>0.02</b> )	0.80 (< <b>0.0001</b> )	0.26 ( <b>0.002</b> )	0.33 (0.27)	-0.34 (< <b>0.0001</b> )
DNA (µg mg <sup>-1</sup> )		-0.28 (< <b>0.0001</b> )	0.59 (< <b>0.0001</b> )	-0.01 (0.97)	-0.43 (< <b>0.0001</b> )
RNA:DNA			-0.25 ( <b>0.0002</b> )	0.31 (0.30)	-0.12 (0.08)
DNA:DW				0.03 (0.93)	-0.67 (< <b>0.0001</b> )
Energy (cal g <sup>-1</sup> )					0.07 (0.81)

## **DISCUSSION**

There was agreement among indices consistent with the notion that marshes flooded by Caernarvon were capable of producing optimum growth habitat for *G. affinis*. This conclusion was also supported by growth rates in the field that matched those found for fish fed *ad libitum* in the laboratory. Although morphometric and biochemical indices were generally not directly correlated in the experiments, their response patterns were similar in terms of the direction and magnitude of change. The indicators showed clear differences in the response time and sensitivity. Specifically, daily growth, length-weight condition, mean weight and energy density measures all showed a relatively rapid response to treatments, while RNA:DNA response lagged somatic indices by approximately one week. While all of the indices appear to be potential candidates as field-based indicators for assessment of fisheries resources, understanding the response time of each indicator is key for selecting the most appropriate index, analysis, and interpretation of results.

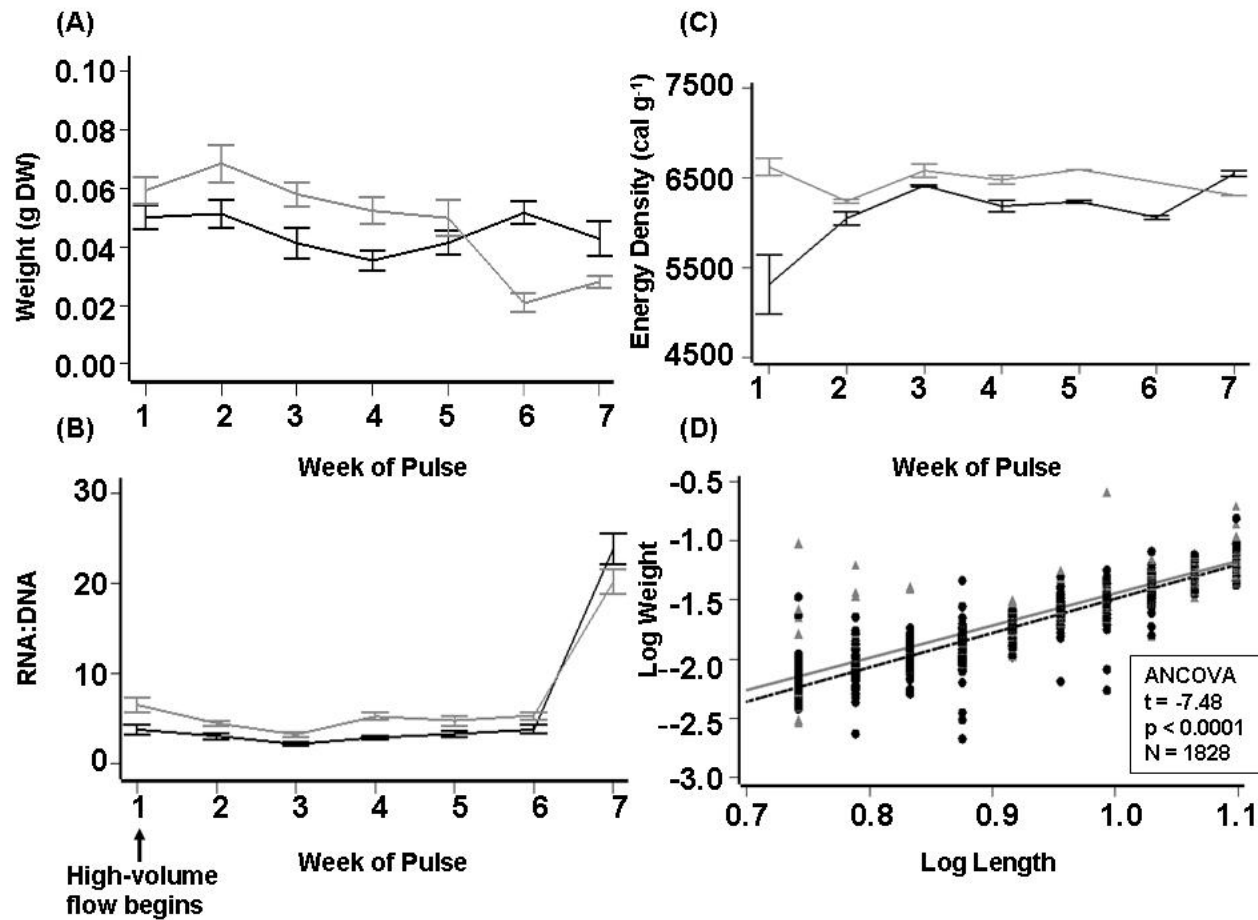


Fig. 4.4. Field experiment 2: Through-pulse field collection. Comparison of (A) weekly mean weight (g DW) and (B) RNA:DNA indices, as well as (C) weekly energy density (cal g<sup>-1</sup>) and (D) length-weight condition for wild-caught *Gambusia affinis* through a seven week freshwater pulse event in upper Breton Sound, Louisiana. Inflow fish were captured weekly in flooded marsh habitat downstream from the Caernarvon Freshwater Diversion beginning on the first day of the pulse event. Reference fish were captured weekly in flooded marsh habitat unaffected by the freshwater pulse. Comparisons of growth rate and RNA:DNA are based on N = 208 fish (104 inflow, 104 reference), and comparisons of energy density and length-weight condition are based on N = 1,828 fish. In all graphs, black represents inflow fish, and gray represents reference fish.

## Growth and Habitat Quality

There was agreement among the indices that marshes flooded by Caernarvon were capable of producing rapid growth in experimental fish and represented energetically valuable habitat to support trophic transport. Assuming that laboratory conditions for fed fish (*ad libitum* feeding, no predation, stable water temperature) resulted in optimum growth rates, the results of the enclosure experiment suggest that inflow marshes were capable of producing optimum growth of *G. affinis*. Compared with other studies, *G. affinis* in inflow marshes grew at a rate comparable to other estuarine resident (*G. affinis*, Wurtsbaugh & Cech 1983; *Fundulus heteroclitus*, Kneib & Stiven 1978) and transient species (*S. ocellatus*, Stunz et al. 2002; *Leiostomus xanthurus*, Weinstein & Walters 1981; *Pseudopleuronectes americanus*, Sogard 1992; Meng et al. 2000; *Tautoga onitis*, Sogard 1992). The energy density index also showed positive growth and energy in inflow throughout the pulse event, and *G. affinis* in inflow marshes contained comparable amounts of energy as other species of forage fish (Perez 1994, Tierney et al. 2002, Wanless et al. 2005).

Weekly field-collection results showed two interesting growth-related pulses. During weeks 1 – 3 of the freshwater pulse, there was a significant increase in energy density in fish captured in the inflow area, and despite this fact, all other indices showed greater fish size and condition in reference marshes. This initial rapid increase in energy immediately following the start of the pulse may be capturing a feeding pulse in response to fish gaining access to valuable flooded habitat, thus providing an immediate indication of an increase in food availability, an important component of habitat quality. A second pulse occurred during week five of the freshwater pulse, when somatic growth indicators showed a shift to greater nekton size and condition in inflow fish, and the biochemical indicators (RNA:DNA, energy density) lagged by one week. This growth shift may represent either a delayed response to the increased food

availability provided by the freshwater pulse or a secondary peak in prey items for *G. affinis*, such as invertebrates and mosquitoes. Studies have shown that flood events temporarily decrease invertebrate abundance in aquatic systems; however populations recover sometime within days to months (Dodds et al. 2004). One study on intermittently flooded streams found that peak benthic macroinvertebrate density and diversity were found 40-60 d after flood events (Dodds et al. 2004). Flooding has also been shown to stimulate the laying and hatch of mosquito eggs, and evidence suggests that full cohort development for mosquitoes at similar water temperatures as seen in this study, takes from 30-40 d (Fontanarrossa et al. 2000).

Alternatively, weekly sampling may not have captured a shift in habitat quality but rather a difference in the size distribution of fish resulting from life history plasticity in *G. affinis*. Experimental fish in the reference area may be on a different developmental schedule than fish in the inflow area, and larger individuals in the reference area early in the early weeks of the pulse may have been gravid overwintering females that produced young and died off by the end of the collection period. A die-off of large adult fish would leave smaller, faster growing fish in the population and may explain the negative temporal growth relationships (length and weight) found during the weekly collections, as well as the sudden increase in RNA:DNA during week seven in the reference area. It is not uncommon to see variability in size, growth, and population dynamics in fishes, and particularly Poeciliids, that are collected in close proximity to one another, especially when there are differences in hydrologic disturbance patterns (Trendall 1983).

The field experiments were not able to document why the shift in growth occurred, as multiple enclosure experiments throughout the pulse would have been necessary to corroborate the results from discrete samples collected prior to week 6. However, this lagged shift, as well as the lagged response by the biochemical indicators, shows the importance of examining habitat



quality over appropriate temporal scales (Rountree & Able 2007) and suggests caution in only selecting one indicator or experimentation method for interpretation and analysis. These results also highlight the potential importance of the duration of seasonal flood pulses for ecosystem productivity (Odum et al. 1995).

### **Growth Indices**

Morphometric and biochemical indices were generally not directly correlated. However, except for the timing of changes, the indices produced general agreement in response and pattern. This is an interesting finding because correlations are often used to assess growth indices, but relationships are often time-dependent. The results highlight the need to look at the time-evolution of response. For example, RNA:DNA did not appear to be a good predictor of growth when based on a direct correlation with morphometric indices. However, the response pattern of RNA:DNA generally agreed with somatic growth (mean weight, length, length-weight condition) in all experiments. Interestingly, the response pattern for RNA:DNA consistently lagged that of the morphometric indices by about one week. This lag was unexpected, as biochemical indices and specifically RNA:DNA are held to be highly sensitive to growth, with rapid response times (1-2 d; Richard et al. 1991; Rooker et al. 1997).

Despite its high variability, RNA:DNA appeared to produce relatively consistent results across all experiments in this study, and helped provide a comprehensive view of fish growth, especially when reliance on morphometric indices alone led to questions of interpretation. For example, during the field collections experiment, while there was some question as to what drove the shift in size distribution, RNA:DNA agreed with the energy density index, a measure of energy-rich protein and lipid tissue, which showed significant positive growth through the pulse in inflow fish. This consistency was not expected, as RNA:DNA has not typically been a successful index in wild and adult fish because it relies on the unstable RNA molecule and is

sensitive to cellular processes involved with reproduction and cellular growth dynamics as fish age (Bergeron 1997, Buckley et al. 1999). Therefore, the index has been most successful at predicting growth in larval and juvenile stages and even-age cohorts when the majority of anabolic energy is devoted to somatic growth and ontogenetic variability is minimized (Ferron & Leggett 1994; Bergeron 1997; Buckley et al. 1999).

Because of the range of water temperatures found in the field studies (enclosure experiment  $\sim 6^{\circ}\text{C}$ ; field collection  $\sim 16^{\circ}\text{C}$ ), temperature had the potential to affect RNA:DNA as a growth indicator in the field experiment. Temperature affects fish growth (Buckley et al. 1999; Searcy et al. 2007) and RNA:DNA by affecting the rate of cellular rate of protein translation (Buckley et al. 1999; Caldarone et al. 2003; Mercado-Allen et al. 2006). The analyses, however, showed that water temperatures were not different by treatment and appeared to fluctuate in unison both within and across treatment areas, likely causing growth variability to be expressed in fish across the entire study area. For example, temperature may have been a factor that caused the sudden and large increase in RNA:DNA in the reference area, that mirrored that in the inflow area during week seven of the field experiment. Week seven witnessed the highest temperatures recorded during the study in both inflow and reference areas. Although, temperature did not to affect the usefulness of RNA:DNA when viewed temporally, the temperature effect is important to consider when designing experiments or using growth indices where temperature ranges and fluctuations may be mismatched. At the same time, while temperature can not be ignored in any growth study, food availability has been shown to affect growth and the expression of RNA:DNA more than temperature (Buckley et al. 1984), suggesting that, as long as temperature fluctuations across the study area are occurring in unison and affecting all study fish simultaneously, comparisons of fish growth with RNA:DNA is appropriate.

Due to its dependence on body weight, the relative DNA content index was able to detect growth changes when significant changes in weight occurred and does not appear to be a very sensitive or useful indicator. During the field collection experiment, although relative DNA content showed a significant relationship that corresponded to the loss of weight in reference fish, the indicator provided no additional information that helped provide a more comprehensive view of fish growth in discretely caught wild fish.

### **Conclusions**

This growth study showed that marshes flooded by restored freshwater pulsing were capable of producing optimum growth and energetically valuable habitat to support trophic transport, and, despite high variability, many common morphometric and biochemical growth indices led to the same conclusions as to the habitat quality for wild *G. affinis*. These findings (1) highlight the importance of understanding the sensitivity of individual indices as well as their response time to changes in habitat quality; and (2) contrast with other field studies where the high variability of RNA:DNA values from one-time sampling of wild fish precluded the ability of the index to integrate habitat effects (e.g. Rooker et al. 1997). These results also suggest that any of the growth indices measured on discretely-caught wild fish, are useful as indicators to monitor and assess habitat quality and draw general conclusions about the effects of restoration on habitat quality for nekton, as long as the sampling period is long enough to incorporate both the sensitivity of the techniques and delayed habitat effects that result from the management actions. Further studies in this area should incorporate multiple targeted short-term growth experiments to supplement discrete field sampling in order to provide comparison of the indices over longer time scales that would further refine our understanding of habitat function and benefit rapid assessment techniques. This is an area of applied research that will be of great benefit to wetland habitat restoration and management programs.

## **LITERATURE CITED**

- Able KW (1999) Measures of juvenile fish habitat quality: examples from a national estuarine research reserve. Pages 134-147 in L. R. Benaka, editor. Fish habitat: essential fish habitat and rehabilitation. Am Fish Soc Symp, Bethesda, Maryland
- Amara R, Meziane T, Gilliers C, Hermel G, Laffargue P (2007) Growth and condition indices in juvenile sole *Solea solea* measured to assess the quality of essential fish habitat. Mar Ecol Prog Ser 351:201-208
- Anderson RO, Neumann RM (1996) Length, weight, and associated structural indices. Pages 447-476 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2<sup>nd</sup> edition. American Fisheries Society, Bethesda, Maryland
- Bergeron JP (1997) Nucleic acids in ichthyoplankton ecology: a review, with emphasis on recent advances for new perspectives. J Fish Biol 51:284-302
- Buckley LJ, Turner SI, Halavik TA, Smigielski AS, Drew SM, Lawrence GC (1984) Effects of temperature and food availability on growth, survival, and RNA-DNA ratio of larval sand lance (*Ammodytes americanus*). Mar Ecol Prog Ser 15:91-97
- Buckley L, Caldarone E, Ong TL (1999) RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia 401:265-277
- Bulow FJ (1987) RNA-DNA ratios as indicators of growth in fish: a review. Pages 45-64 in R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. The Iowa State University Press, Ames, Iowa
- Caldarone EM, St. Onge-Burns JM, Buckley LJ (2003) Relationship of RNA/DNA ratio and temperature to growth in larvae of Atlantic cod (*Gadus morhua*). Mar Ecol Prog Ser 262:229-240
- Caldarone EM, Clemmesen CM, Berdalet E, Miller TJ, Folkvord A, Holt GJ, Pilar Olivar M, Suthers IM (2006) Intercalibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. Limnol Oceanogr - Meth 4:153-163
- Craig JF, Kenley MJ, Talling JF (1978) Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. Freshwater Biol 8:585-590
- Dodds WK, Gido K, Whiles MR, Fritz KM, Matthews WJ (2004) Life on the edge: the ecology of Great Plains prairie streams. Bioscience 54:205-216.
- Ferron A, Leggett WC (1994) An appraisal of condition measures for marine fish larvae. Adv Mar Biol 20:217-303
- Flath LE, Diana JS (1985) Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans Am Fish Soc 114:328-337

- Fontanarrosa MS, Marinone MC, Fischer S, Orellano PW, Schweigmann N (2000) Effects of flooding and temperature on *Aedes albifasciatus* development time and larval density in two rain pools at Buenos Aires University city. *Memorias Do Instituto Oswaldo Cruz* 95:787-793
- Gilliers C, Amara R, Bergeron JP, Le Pape O (2004) Comparison of growth and condition indices of juvenile flatfish in different coastal nursery grounds. *Environ Biol Fish* 71:189-198
- Goede RW, Barton BA (1990) Organismic indices and an autopsy-based assessment as indicators of health and condition of fish. *Am Fish Soc Symp* 8:93-108
- Hartman KJ, Brandt SB (1995) Estimating energy density in fish. *Trans Am Fish Soc* 124:347-355
- Kneib RT (2000) Saltmarsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. Pages 267-291 *in* M. P. Weinstein and D. A. Kreeger, editors. *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Boston, Massachusetts
- Kneib RT, Stiven AE (1978) Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. *J Exp Mar Biol Ecol* 31:121-140
- La Peyre MK, Gossman B, Nyman JA (2007) Assessing functional equivalency of nekton habitat in enhanced habitats: comparison of terraced and untterraced marsh ponds. *Estuaries and Coasts* 30:526-536
- Lane RR, Day JW Jr, Marx BD, Reyes E, Hyfield E, Day JN (2007) The effects of riverine discharge on temperature, salinity, suspended sediment and chlorophyll a in a Mississippi delta estuary measured using a flow-through system. *Est Coast Shelf Sci* 74:145-154
- Lorenzen K, Enberg K (2002) Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *P Roy Soc Lond B Bi* 269:49-54
- Madon SP (2008) Fish community responses to ecosystem stressors in coastal estuarine wetlands: a functional basis for wetlands management and restoration. *Wetl Ecol Manage* 16:219-236
- Meng L, Gray C, Taplin B, Kupcha E (2000) Using winter flounder growth rates to assess habitat quality in Rhode Island's coastal lagoons. *Mar Ecol Prog Ser* 201:287-299
- Mercado-Allen R, Kuropat C, Caldarone EM (2006) A model to estimate growth in young-of-the-year tautog, *Tautoga onitis*, based on RNA/DNA ratio and seawater temperature. *J Exp Mar Biol Ecol* 329:187-195
- Odum WE, Odum EP, Odum HT (1995) Nature's pulsing paradigm. *Estuaries* 18:547-555

- Oliva-Paterna FJ, Miñano PA, Torralva M (2003) Habitat quality affects the condition of *Barbus sclateri* in Mediterranean semi-arid streams. *Environ Biol Fish* 67:13-22.
- Pederson RA (1971) DNA content, ribosomal gene multiplicity, and cell size in fish. *J Exp Zool* 177:65-78
- Perez MA (1994) Calorimetry measurements of energy value of some Alaskan fishes and squids. U.S. Department of Commerce, NOAA Technical Memorandum. NMFS-AFSC-32
- Piazza BP, La Peyre MK (2007) Restoration of the annual flood pulse in Breton Sound, Louisiana, USA: habitat change and nekton community response. *Aquat Biol* 1:109-119
- Piazza BP, La Peyre MK, Quantifying the nekton subsidy provided by riverine pulsing: an approach and example for a southeastern US estuary. *Wetlands*, In Review
- Richard P, Bergeron JP, Boulhic M, Galois R, Person-Le Ruyet J. (1991) Effect of starvation on RNA, DNA and protein content of laboratory-reared larvae and juvenile of *Solea solea*. *Mar Ecol Prog Ser* 72:69-77
- Rooker JR, Holt GJ, Holt SA (1997) Condition of larval and juvenile red drum (*Sciaenops ocellatus*) from estuarine nursery habitats. *Mar Biol* 127:387-394
- Rountree RA, Able KW (2007) Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. *Aquat Ecol* 41:25-45
- Rozas LP (1995) Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18:579-590
- Rozas LP, Minello TJ, Munuera-Fernández E, Fry B, Wissel B (2005) Macrofaunal distributions and habitat change following winter-spring releases of freshwater into the Breton Sound estuary, Louisiana (USA). *Est Coast Shelf Sci* 65:319-336
- Searcy SP, Eggleston DB, Hare JA (2007) Is growth a reliable indicator of habitat quality and essential fish habitat for a juvenile estuarine fish? *Can J Fish Aquat Sci* 64:681-691
- Snedden GA, Cable JE, Swarzenski C, Swenson E (2007) Sediment discharge into a subsiding Louisiana deltaic estuary through a Mississippi River diversion. *Est Coast Shelf Sci* 71:181-193
- Sogard SM (1992) Variability in growth rates of juvenile fishes in different estuarine habitats. *Mar Ecol Prog Ser* 85:35-53
- Stunz GW, Minello TJ, Levin PS (2002) Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitats. *Mar Ecol Prog Ser* 238:227-236

- Teal L.R, de Leeuw JJ, van der Veer HW, Rijnsdorp AD (2008) Effects of climate change on growth of 0-group sole and plaice. *Mar Ecol Prog Ser* 358:219-230
- Tierney M, Hindell M, Goldsworthy S (2002) Energy content of mesopelagic fish from Macquarie Island. *Antarctic Science* 14:225-230
- Trendall JT (1983) Life history variation among experimental populations of the mosquitofish, *Gambusia affinis*. *Copeia* 1983:953-963
- Vila-Gispert A, Moreno-Amich R (2001) Mass-length relationship of Mediterranean barbel as an indicator of environmental status in southwest European stream ecosystems. *J Fish Biol* 59:824-832
- Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1-8
- Weber LP, Higgins PS, Carlson RI, Janz DM (2003) Development and validation of methods for measuring multiple biochemical indices of condition in juvenile fishes. *J Fish Biol* 63:637-658
- Weinstein MP, Walters MP (1981) Growth, survival and production in young-of-the-year populations of *Leiostomus xanthurus* Lacépède residing in tidal creeks. *Estuaries* 4:185-197
- Wurtsbaugh WA, Cech JJ Jr (1983) Growth and activity of juvenile mosquitofish: temperature and ration effects. *Trans Am Fish Soc* 112:653-660
- Zapfe GA, Rakocinski CF (2008) Coherent growth and diet patterns in juvenile spot (*Leiostomus xanthurus* Lacépède) reflect effects of hydrology on access to shoreline habitat. *Fish Res* 91:107-111

## CHAPTER 5

### THE EFFECT OF HURRICANE KATRINA ON NEKTON COMMUNITIES IN THE TIDAL FRESHWATER MARSHES OF BRETON SOUND LOUISIANA, USA\*

#### INTRODUCTION

Resource pulses are defined as rare, brief, and intense phenomena that cause significant ecosystem perturbation, including change in biotic community structure (Yang et al. 2008).

Many resource pulses are driven by climatic events, and the corresponding change in community structure can be direct or indirect, result either from the pulsed delivery of resources, physical disturbance, or both, and persist for varying lengths of time (Yang et al., 2008). Understanding the effects of this pulse-induced change on community structure, including its persistence through time, will provide information on ecosystem resiliency (Switzer et al., 2006).

Hurricanes are examples of climatically-induced pulses that result in periodic and often intense ecosystem disturbance. Landfalling hurricanes affect biotic community structure in both terrestrial and aquatic ecosystems through the import of chemical and biological resources and direct physical habitat change (Cahoon, 2006; Yang et al., 2008). For example, hurricanes have direct and indirect effects on tropical forest communities both from the input of nutrients from leaf fall as well as the physical change in forest structure from tree falls (Yang et al., 2008).

Because of their position in the landscape, estuaries are especially vulnerable to hurricane-induced pulse events. When a hurricane makes landfall, it not only brings an intense pulse of wind and precipitation from the storm system but also a large storm surge that inundates the estuary with sea water, resuspended sediments, and nutrients (Nyman et al., 1995; Cahoon, 2006). This combination of factors causes physical and chemical changes to the estuary that affect nekton communities (Greenwood et al., 2006; Stevens et al., 2006; Paperno et al., 2006; Switzer et al., 2006). Aquatic habitats have shown resilience to hurricane effects, with nekton

\*Reprinted by permission of *Estuarine, Coastal and Shelf Science*



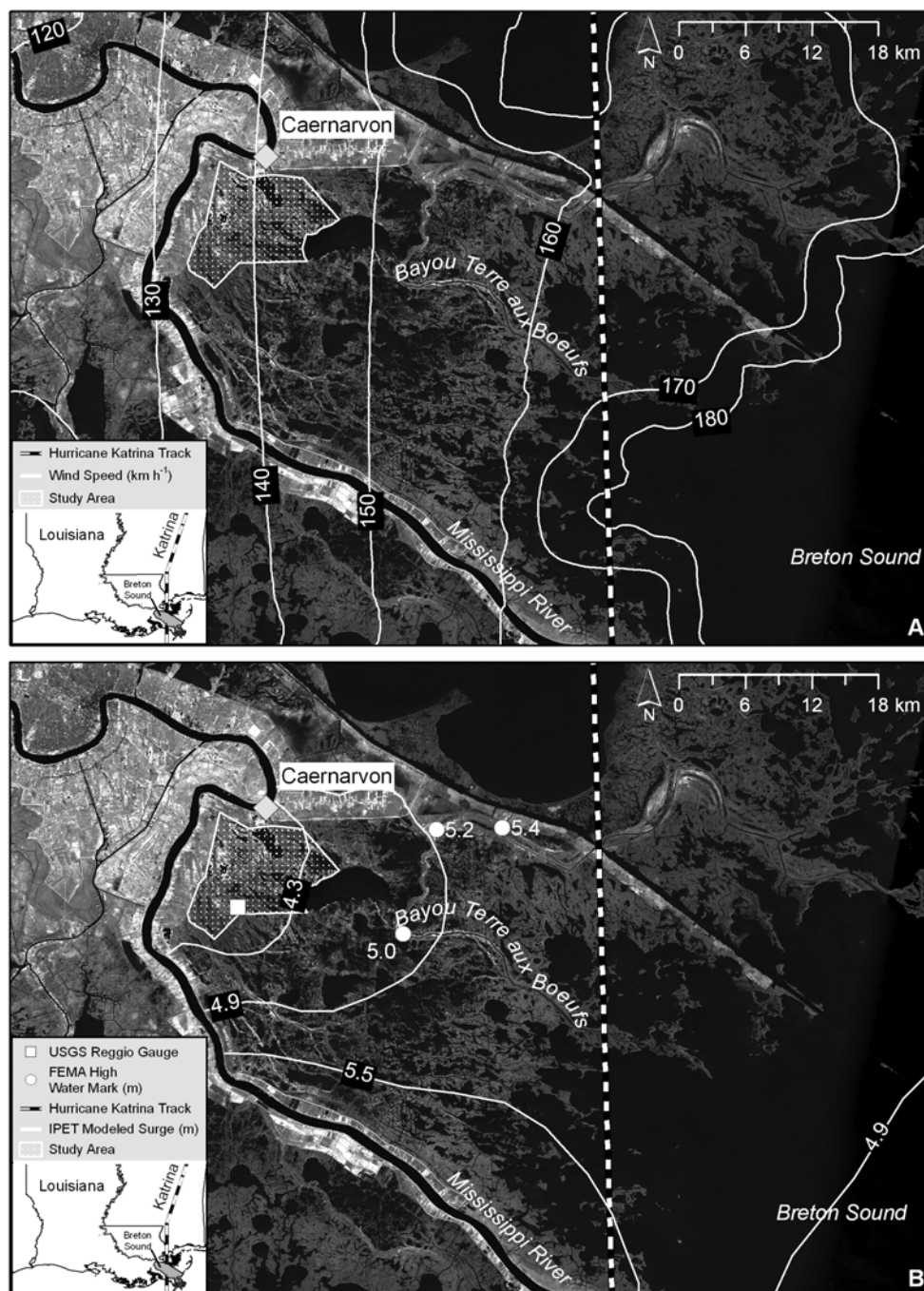
communities returning to pre-hurricane conditions in a matter of weeks to months (Paperno et al., 2006). However, many of these studies in estuarine habitat take place in brackish and saline zones or in lagoonal estuaries, where hurricane effects are largely chemical (e.g. hypoxia, salinity effects) and quickly mitigated (Switzer et al., 2006). In contrast, relatively little is known about the influence of hurricanes on nekton communities in tidal freshwater areas where the physical habitat disturbance to vegetated marsh habitat can be extensive and may not be readily mitigated.

We measured the immediate and enduring effects of hurricanes on nekton community structure in tidal freshwater habitat of the upper Breton Sound estuary, Louisiana. The objective was to document effects of a direct hit from a major hurricane on nekton communities in tidal freshwater, 6-month and 18-month post hurricane. Here, we describe the pre- and 6-month and 18-month post-hurricane community structure of estuarine nekton during annual spring riverine flooding events in upper Breton Sound estuary.

### **Study Area**

We studied effects of hurricane passage on nekton communities by comparing nekton assemblages before (spring 2005) and after (spring 2006 and 2007) the passage of Hurricane Katrina in upper Breton Sound estuary, Louisiana (Fig. 5.1). Breton Sound is a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana. It is microtidal and consists of bays, lakes, bayous, canals, and fresh, intermediate, brackish, and saline marsh types. The upper estuary is separated into east and west components, geographically and hydrologically, by Bayou Terre aux Boeufs, a relic Mississippi River distributary. Dominant emergent vegetation in upper basin marshes consists of *Spartina patens* (saltmeadow cordgrass) and *Schoenoplectus americanus* (chairmaker's bulrush).

Fig. 5.1. Maps showing Breton Sound estuary, Louisiana and (A) wind speed ( $\text{km h}^{-1}$ ) and (B) storm surge height (m) during Hurricane Katrina. The white stippled area in both maps delineates the boundary of the tidal freshwater marshes where nekton were sampled during this study. The storm track of Hurricane Katrina is shown as a dashed black and white line on both the maps and inset. The square on panel B indicates the position of the United States Geological Survey (USGS) National Water Information System station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253). Wind speed data are from NOAA, Atlantic Oceanographic and Meteorological Laboratory ([http://www.aoml.noaa.gov/hrd/Storm\\_pages/katrina2005/wind.html](http://www.aoml.noaa.gov/hrd/Storm_pages/katrina2005/wind.html)). Water level contours are based on an ADCIRC coastal storm surge model and are modified from US Army Corps of Engineers (2006; <https://ipet.wes.army.mil>) and Keim and Muller (In Press). Water level points (white dots) are observed high water marks from the Federal Emergency Management Agency (FEMA 2006, map B-12). Background image (Landsat Thematic Mapper 5) is from October 28, 2006.



We studied the effects of the hurricane pulse on nekton communities in emergent marshes subject to flooding (inflow marshes) from the Caernarvon Freshwater Diversion structure (Caernarvon; Fig. 5.1). The structure is located at the head of Breton Sound and is capable of delivering substantial amounts of fresh water ( $227 \text{ m}^3 \text{ s}^{-1}$ ) and allochthonous sediments ( $4.5 \times 10^8 \text{ kg y}^{-1}$ ) from the Mississippi River to the basin (Snedden et al. 2007a).

Yearly experimental high-flow freshwater pulsing of the diversion structure began in spring 2001 to simulate seasonal flood-pulse events. Pulses release periodic large fluxes of Mississippi River water into the basin and are capable of inundating upper basin marshes ( $\sim 5,700$  ha) for several days (Snedden et al., 2007a). Without the riverine pulse, inundation of upper basin marshes is dominated by meteorological forcing (Snedden et al., 2007b).

Hurricane Katrina made its first Louisiana landfall on August 29, 2005 in Plaquemines Parish just south of Buras, Louisiana as a strong Category 3 (Saffir-Simpson scale – maximum = Category 5) storm, with sustained wind speeds of approximately  $205 \text{ km h}^{-1}$  ( $57 \text{ m s}^{-1}$ ) and a central pressure of 920 mb (92 000 Pa). The northerly storm track of Katrina took it directly across Breton Sound estuary on its way to a second northern Gulf coast landfall near the Louisiana – Mississippi border (Fig. 5.1). Sustained wind speed when the storm crossed Breton Sound estuary was estimated at  $122 - 194 \text{ km h}^{-1}$  ( $34 - 54 \text{ m s}^{-1}$ ). Storm surges from 5 – 6 m were recorded at the mouth of the Mississippi River, across Breton Sound, and into New Orleans, Louisiana (Graumann et al., 2005; Hsu et al., 2006; Fritz et al., 2007). Hurricane Rita, which made landfall approximately one month later (September 24, 2005) along the Louisiana/Texas border as a Category 3 (Saffir-Simpson scale) hurricane, did not directly impact Breton Sound like Hurricane Katrina. However, the westerly track of this storm across the Gulf of Mexico brought an additional storm surge ( $> 1 \text{ m}$ ) to Breton Sound (Day et al., 2007). The physical effects of Hurricane Katrina on Breton Sound were stark, with massive loss of emergent marsh habitat, especially in the upper basin ( $\sim 106 \text{ km}^2$ ; Barras, 2007), and the storm converted large areas of vegetated marsh into shallow open lakes with mud bottoms and large balls of rolled detrital wrack (Fig. 5.2).

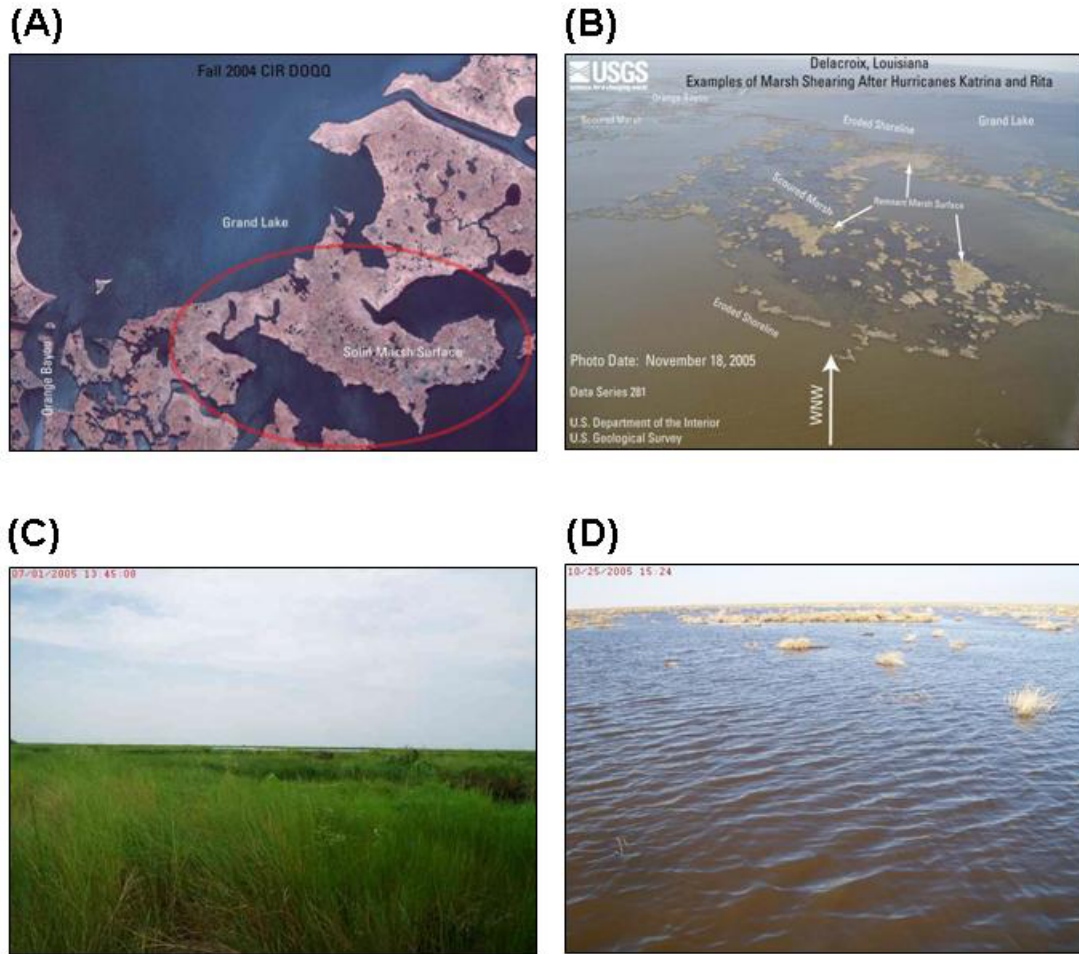


Fig. 5.2. Photographs showing the physical habitat change due to Hurricane Katrina. The first set of photographs (A,B) illustrate the large scale vegetated marsh loss that occurred in Breton Sound estuary as a result of Hurricane Katrina. The area inside the red oval in Fig 2A is the area in Fig 2B. Also shown is a small-scale illustration of the pre- (C) and post-hurricane (D) condition of the marshes sampled during this study. Photos A and B are taken from Barras (2007), and photos C and D are courtesy of S. Piazza, U.S. Geological Survey, National Wetlands Research Center, Coastal Restoration Field Station, Baton Rouge, LA.

## METHODS

Storm surge effects in upper Breton Sound were determined from data obtained from the United States Geological Survey (USGS) National Water Information System (<http://waterdata.usgs.gov/usa/nwis/>). Specifically, we obtained salinity (practical salinity units; psu) and water level (m NAVD 88) data for upper Breton Sound from 2005-2007 from the station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253; Fig. 5.1B).

We collected nekton samples in vegetated marsh habitat through winter-spring pulsed freshwater releases in 2005 – 2007. Sampling occurred in flooded marshes directly downstream from the Caernarvon Freshwater Diversion (inflow marshes). In 2005, nekton sampling occurred from February 14 – 28 and March 12 – 28. Sampling in 2006 occurred from March 22 – 28 and April 18 – 23. Due to equipment and logistical problems nekton were sampled in 2007 only on March 24 – 25. Discharge from Caernarvon was similar during each sampling period ( $\sim 184 \text{ m}^3 \text{ s}^{-1}$ ).

Sites were sampled with a 1.14 m cylindrical ( $1 \text{ m}^2$ ) drop sampler. At each site, nekton were collected and environmental data were recorded. A complete description of the sampling methodology, including laboratory processing of samples is reported in Piazza and La Peyre (2007).

### **Data Analysis**

Nekton and environmental data were tested for normality with the Shapiro-Wilks test. Nekton density and biomass were log transformed to achieve normality. Data are reported as mean  $\pm$  SE, and significance level is reported at  $\alpha = 0.05$ , unless indicated differently.

#### Environmental Conditions

Differences in discrete environmental variables (salinity, dissolved oxygen, temperature, stem density, turbidity, water depth) were compared by year using multivariate analysis of variance (MANOVA). Significant MANOVA models were investigated further with univariate ANOVA.

#### Nekton Density, Biomass, Diversity

ANOVA (PROC MIXED) was used to test for statistical differences in density, biomass, and diversity among years. Difference in least squared means was used to compare density and diversity among years. Alpha ( $\alpha$ ) diversity was calculated with both Shannon-Wiener diversity

( $H'$ ) and evenness ( $E$ ), and Sorenson's Similarity Index ( $C_s$ ) was used to compare beta ( $\beta$ ) diversity among years (Magurran 1988).

### Nekton Communities

To determine the effect of the hurricane pulse on estuarine nekton communities, each species was assigned a residence status based on natural history characteristics obtained from the literature and fishbase (Froese and Pauly, 2008; [www.fishbase.org](http://www.fishbase.org)). Tidal freshwater/Resident (T/R) species were defined as those that spend their entire life cycle within the estuary and are abundant in the tidal freshwater portion of the estuary. This group include species that are both stenohaline (e.g. *Lepomis macrochirus*) and euryhaline (*Poecilia latipinna*), however, most species are closely tied to the flooded marsh surface and exhibit small home ranges (Kneib 2000; Piazza and La Peyre, 2007). Brackish/Migrant (B/M) species were defined as those that spend at least a portion or all of their life cycle in the estuary, but typically in more saline water than tidal freshwater species (Kneib, 2000). Migrating members of this group spawn on the continental shelf and migrate into the estuary to spend the juvenile portion of their life cycle. Members of this group that spend their entire life cycle in the estuary spawn in polyhaline waters but may move into fresher portions of the estuary. Members of this group were generally either pelagic (e.g. *Anchoa mitchilli*) or bottom-oriented (e.g. *Gobiosoma bosc*) and less associated with the marsh surface than T/R species.

## **RESULTS**

### **Environmental Characteristics**

A strong pulse of marine water was propagated into upper Breton Sound estuary, during and immediately following passage of Hurricane Katrina (Fig. 5.3). During this time, the water level and salinity were approximately 3 m and 15 psu, respectively, at the Reggio gauge. After Katrina, storm surge estimates > 5 m were documented in Breton Sound by the US Federal

Emergency Management Agency (FEMA 2006; Fig. 1). Water levels returned to pre-hurricane conditions relatively quickly; however salinity in the upper estuary remained elevated above 3 psu into January 2006, due to the additive effects of Hurricane Rita and a period of moderate to severe drought that began in early 2005 and persisted through the end of the year (U.S. Drought Monitor, 2005; <http://www.drought.unl.edu/>).

By the time we sampled nekton in late March 2006, environmental conditions had returned to levels typical of early spring in upper Breton Sound (Lane et al., 2007; Table 5.1). However, three trends deserve particular attention. Mean turbidity doubled between 2005 and 2006. Additionally, mean water depth increased and mean vegetative cover decreased between 2005 and 2007 (Table 5.1).

### **Nekton Density, Biomass, Diversity, and Communities**

A total of 20 057 individuals were collected over the three year study period. Nekton density was significantly different by year ( $F_{2,274} = 8027$ ,  $p < 0.0003$ ), with a pronounced increase in 2006 (Fig. 5.4a). Mean nekton biomass ( $\text{g m}^{-2}$ ;  $19.76 \pm 1.83$  SE,  $N = 290$ ) was also significantly different by year ( $F_{2,274} = 7.03$ ,  $p < 0.001$ ), and followed the same pattern as nekton density. The increase in density during the 2006 sampling year was largely driven by high densities of riverine grass shrimp (*Palaemonetes paludosus*) and opossum shrimp (*Taphromysis bowmani*) in the spring following Hurricane Katrina (Table 5.2). Although previously not



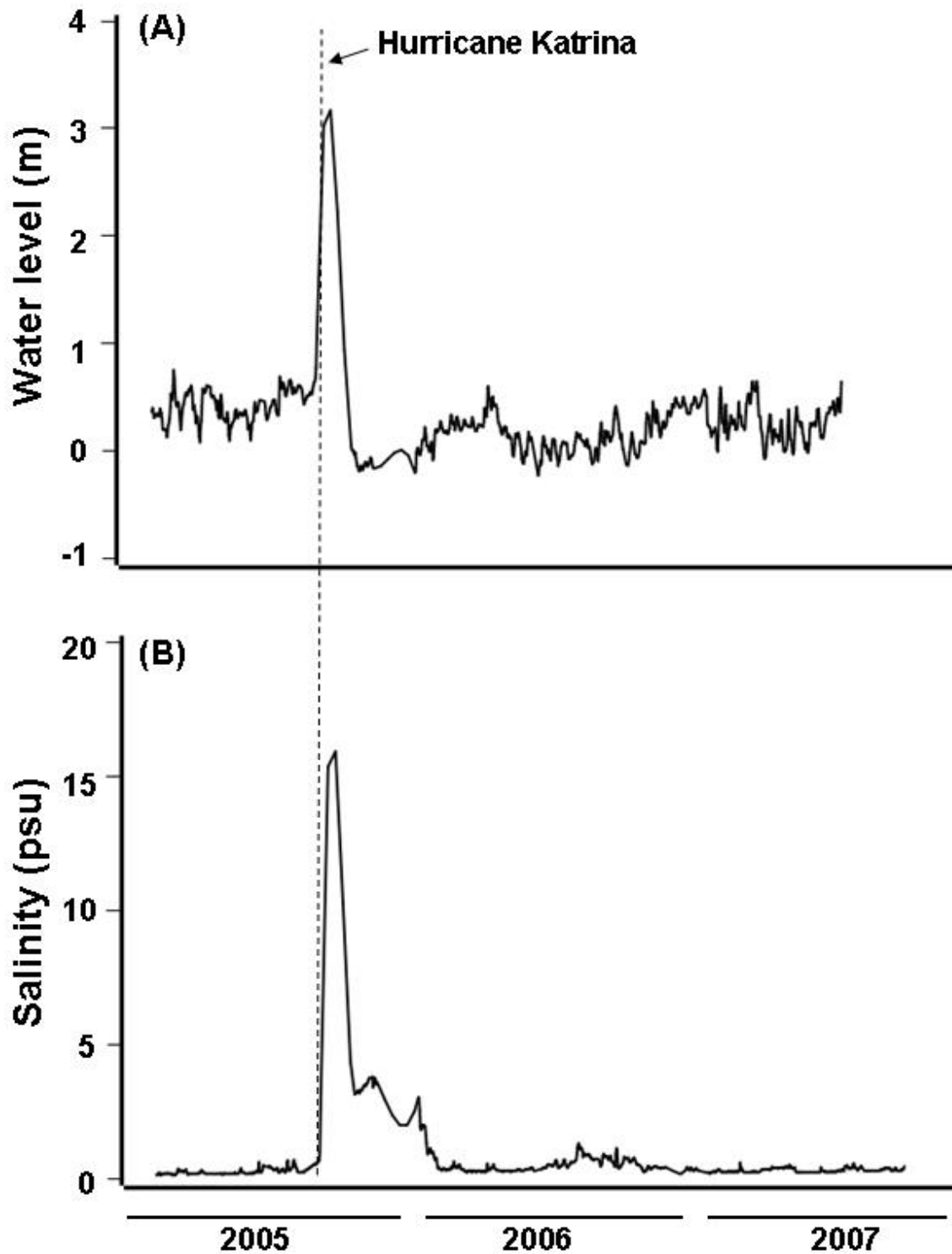


Fig. 5.3. Hydrographs of continuous A) water level and B) salinity from January 1, 2005 – December 31, 2007, taken at United States Geological Survey (USGS) National Water Information System station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253). The vertical dashed line marks the passage of Hurricane Katrina.

Table 5.1. Mean ( $\pm$  SE) and range of environmental characteristics (water temperature, salinity, dissolved oxygen, turbidity, vegetative cover, water depth) measured on the flooded marsh surface in upper Breton Sound estuary, Louisiana during nekton sampling in spring 2005 – 2007 through winter-spring riverine pulse events.

Variable	2005	2006	2007
	N = 141	N = 140	N = 9
	Mean $\pm$ SE (Range)	Mean $\pm$ SE (Range)	Mean $\pm$ SE (Range)
Temperature ( $^{\circ}$ C)	17.88 $\pm$ 0.31 (10.5 - 28.1)	21.9 $\pm$ 0.44 (13.1 - 31.3)	17.2 $\pm$ 1.08 (13.2 - 22.4)
Salinity (psu) <sup>1</sup>	0.2 $\pm$ 0.01 (0.2 - 0.7)	0.2 $\pm$ 0.00 (0.1 - 0.3)	0.2 $\pm$ 0.01 (0.2 - 0.3)
Dissolved Oxygen (mg l <sup>-1</sup> )	3.8 $\pm$ 0.18 (1.0 - 9.4)	3.5 $\pm$ 0.13 (0.5 - 8.1)	8.5 $\pm$ 0.66 (5.8 - 12.7)
Turbidity (NTU) <sup>2</sup>	15.4 $\pm$ 0.77 (0.8 - 50.0)	30.8 $\pm$ 1.32 (10.1 - 82.5)	9.2 $\pm$ 1.53 (5.8 - 20.0)
Vegetative Cover (stems m <sup>-2</sup> )	123.4 $\pm$ 12.23 (0.00 - 618.0)	102.1 $\pm$ 15.9 (0.0 - 1259.0)	15.4 $\pm$ 12.45 (0.0 - 114.0)
Water Depth (mm)	254.5 $\pm$ 10.3 (26.0 - 723.0)	283.2 $\pm$ 14.8 (29.6 - 821.8)	369.4 $\pm$ 55.64 (141.0 - 674.0)

<sup>1</sup> psu = practical salinity units; <sup>2</sup> NTU = nephelometric turbidity units

collected from drop samples, *T. bowmani* was caught in most (62%) samples in 2006, and its presence was still significant in spring 2007 (33%; Table 5.2).

Species richness in upper Breton Sound increased after Hurricane Katrina from 16 taxa spring 2005 to 26 taxa in 2006 and decreased again in 2007 to only 12 taxa (Table 5.2). This increase in species richness in 2006 was driven by an increase in B/M species in spring 2006 samples. Mean Shannon diversity ( $H' = 0.79 \pm 0.02$  SE) and evenness ( $E = 0.63 \pm 0.02$  SE) were

significantly different by year ( $H' - F_{2,274} = 12.00$ ,  $p < 0.0001$ ;  $E - F_{2,256} = 15.06$ ,  $p < 0.0001$ ; Fig. 5.4b).

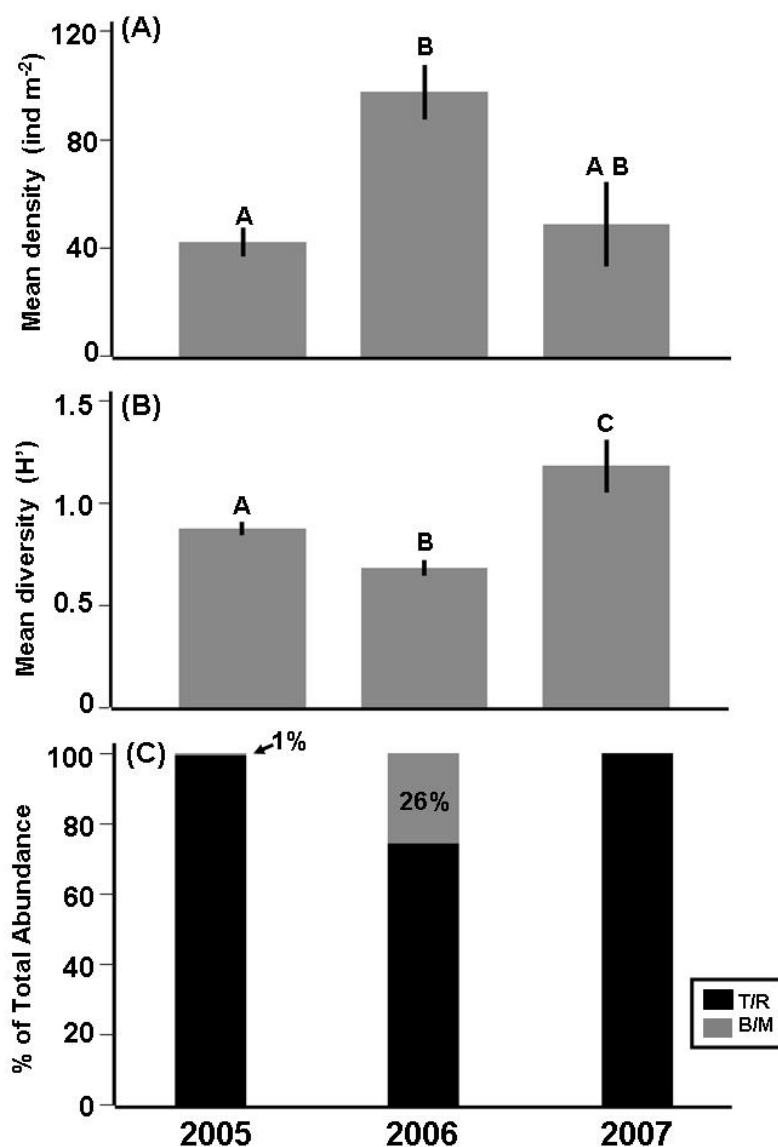


Fig. 5.4. Mean ( $\pm$  SE) A) nekton density (ind. m<sup>-2</sup>), and B) Shannon-Weiner Diversity ( $H'$ ), of nekton caught at flooded marsh sampling sites pre- (spring 2005) and post-Hurricane Katrina (spring 2006, 2007). Capital letters denote significant statistical differences ( $\alpha = 0.05$ ) between years. Graph C shows the percentage of total nekton abundance that belonged to either the Tidal Freshwater/Resident group (T/R; black) or the Brackish/Migrant group (B/M; gray) for the same years. Species were grouped according to salinity tolerance and life-history characteristics, and definitions are provided in the text.

Higher numbers of B/M species were caught in the project area after Hurricane Katrina (Fig. 5.4c). The number of B/M species dropped to pre-storm levels in spring 2007. Resident

Table 5.2. Mean nekton density (ind. m<sup>-2</sup>) and percent occurrence in drop samples by species pre- (2005) and post-Hurricane Katrina (2006, 2007). Nekton were sampled on the flooded marsh surface in upper Breton Sound estuary, Louisiana during winter-spring riverine pulse events in spring 2005-2007. Residence status classification is as follows: T/R = Tidal Freshwater/Resident; B/M = Brackish/Migrant. Definitions for both categories are given in the text.

Species	Common Name	Residence Status	2005		2006		2007	
			(N = 141)	%	(N = 140)	%	(N = 9)	%
Fishes								
<i>Heterandria formosa</i>	Least killifish	T/R	14.0 ± 3.74	64	0.1 ± 0.04	6	6.9 ± 4.24	44
<i>Gambusia affinis</i>	Mosquitofish	T/R	5.27 ± 1.05	49	1.4 ± 0.29	36	6.4 ± 3.55	44
<i>Lucania parva</i>	Rainwater killifish	T/R	2.7 ± 0.69	41	8.0 ± 1.15	64	10.0 ± 5.49	100
<i>Poecilia latipinna</i>	Sailfin molly	T/R	0.6 ± 0.13	21	0.3 ± 0.11	9	0.1 ± 0.11	11
<i>Cyprinodon variegatus</i>	Sheepshead minnow	T/R	0.5 ± 0.13	17	0.2 ± 0.07	7	-	0
<i>Fundulus chrysotus</i>	Golden topminnow	T/R	0.1 ± 0.03	8	-	0	-	0
<i>Fundulus pulvereus</i>	Bayou killifish	T/R	0.02 ± 0.02	1	0.04 ± 0.02	3	-	0
<i>Lepomis macrochirus</i>	Bluegill	T/R	0.1 ± 0.03	6	0.1 ± 0.05	6	0.4 ± 0.24	33
<i>Lepomis punctatus</i>	Spotted sunfish	T/R	0.02 ± 0.02	2	-	0	0.1 ± 0.11	11
<i>Lepomis microlophus</i>	Redear sunfish	T/R	0.01 ± 0.01	1	0.04 ± 0.02	4	0.7 ± 0.55	22
<i>Lepomis megalotis</i>	Longear sunfish	T/R	-	0	-	0	0.1 ± 0.11	11
<i>Anguilla rostrata</i>	American eel	B/M	0.01 ± 0.01	1	-	0	-	0
<i>Notropis</i> spp.	Shiner	T/R	0.01 ± 0.01	1	-	0	-	0
<i>Micropterus salmoides</i>	Largemouth bass	T/R	-	0	0.01 ± 0.01	1	-	0
<i>Anchoa mitchilli</i>	Bay anchovy	B/M	-	0	0.2 ± 0.07	9	-	0
<i>Citharichthys spilopterus</i>	Bay whiff	B/M	-	0	0.01 ± 0.01	1	-	0
<i>Elops saurus</i>	Ladyfish	B/M	-	0	0.02 ± 0.02	1	-	0
<i>Gobiosoma bosc</i>	Naked goby	B/M	-	0	0.2 ± 0.11	5	-	0
<i>Microgobius gulosus</i>	Clown goby	B/M	-	0	0.05 ± 0.03	3	-	0
<i>Menidia beryllina</i>	Inland silverside	B/M	-	0	0.6 ± 0.14	19	-	0
<i>Membras martinica</i>	Rough silverside	B/M	-	0	0.01 ± 0.01	1	-	0
<i>Micropogonias undulatus</i>	Atlantic croaker	B/M	-	0	0.01 ± 0.01	1	-	0
<i>Syngnathus scovelli</i>	Gulf pipefish	B/M	-	0	0.01 ± 0.01	1	-	0
<i>Brevoortia patronus</i>	Gulf menhaden	B/M	-	0	0.01 ± 0.01	1	-	0
<i>Arius felis</i>	Hardhead catfish	B/M	-	0	0.01 ± 0.01	1	-	0

Table 5.2. continued.

Species	Common Name	Residence Status	2005		2006		2007	
			(N = 141)	%	(N = 140)	%	(N = 9)	%
Crustaceans								
<i>Palaemonetes paludosus</i>	Riverine grass shrimp	T/R	16.8 ± 2.74	77	43.6 ± 6.3	79	19.4 ± 4.94	100
<i>Cambarellus</i> spp.	Crayfish	T/R	1.2 ± 0.17	43	0.13 ± 0.06	7	1.9 ± 1.10	56
<i>Procambarus</i> spp.	Crayfish	T/R	0.9 ± 0.12	40	0.26 ± 0.08	10	1.4 ± 0.47	67
<i>Callinectes sapidus</i>	Blue crab	B/M	0.02 ± 0.02	1	0.5 ± 0.07	34	-	0
<i>Menippe adina</i>	Gulf stone crab	B/M	-	0	0.04 ± 0.02	3	-	0
<i>Taphromysis bowmani</i>	Opposum shrimp	T/R	-	0	41.1 ± 6.97	62	1.4 ± 0.80	33

species persisted through the study period, but the following trends were apparent: 1) densities of *Gambusia affinis* and *Heterandria formosa* decreased post-Katrina; and 2) densities of *Lucania parva* increased post-Katrina. Nekton communities in the first spring (2006) following Hurricane Katrina were less similar ( $C_s = 0.57$ ) to pre-hurricane communities (2005) than those of spring 2007, 18 months post-hurricane ( $C_s = 0.71$ ). Interestingly, nekton communities were least similar between spring 2006 and 2007 ( $C_s = 0.53$ ).

## **DISCUSSION**

This study documented higher nekton densities and a shift from a nekton community consisting almost exclusively of Transient freshwater/Resident (T/R) species toward one that included a number of Brackish/Migrant (B/M) species after a direct hit by Hurricane Katrina in August 2005. Differences in nekton density were largely attributed to large catches of *Palaemonetes paludosus* and *Taphromysis bowmani*. *T. bowmani* is a mysid shrimp that was not captured in samples in the spring prior to the storm. The emergence of this species in drop samples, as well as the community shift toward B/M, especially those with pelagic and benthic life history strategies, was likely due to the combination of elevated salinity and the stark loss of vegetated marsh habitat that resulted from the hurricane winds and storm surge. Effects were short lived, as by spring 2007, the nekton community had shifted back to T/R species, and communities were more similar between 2005 and 2007 than between post-hurricane sample dates, despite the lasting loss of vegetated marsh habitat.

### **Nekton Community Change**

Increased nekton density post-hurricane was driven by two shrimp species, *P. paludosus* and *T. bowmani*. Although mysid shrimp are not often considered in studies of estuarine nekton, *T. bowmani* was included in the nekton assemblage in this study because it was an important indicator of the habitat change. As with many mysids, *T. bowmani* is an estuarine animal known

to occur in large schools (shoals) in a range of shallow open water habitats across a full range of salinities including almost freshwater (Price, 1982). Mysid shrimp generally avoid densely vegetated marshes, even during high flooding (Allen, 1982). Therefore, the increased amount of open water observed with the loss of vegetation likely favored assembly and habitat use by mysids, including *T. bowmani*. Assembly pulses and redistribution of shrimp have been shown in past studies, to be due to hurricane-induced habitat change and detrital nutrient pulses in both estuarine and stream habitat (Stevens et al., 2006). Additionally, the conversion of habitat to a more pelagic environment with large balls of decomposing marsh wrack favors plankton production and detrital microbes, both important food sources for mysids (Vilas et al., 2008).

In addition to the change in resource availability, it is also possible that the loss of densely vegetated habitat and high turbidity following Hurricane Katrina may have increased the ability of our sampling gear to capture both *P. paludosus* and *T. bowmani*. Gear efficiency can change in a system due to hurricane-induced change (Greenwood et al., 2006). However, results from 2007 show that densities of *P. paludosus* returned to pre-hurricane levels and the density of *T. bowmani* decreased markedly, despite the enduring absence of vegetated marsh habitat. This suggests that, while a temporary increase in trap efficiency may have been a factor, the density pulses of these two animals were more likely driven by the temporary increase in resource availability from decomposing wrack in 2006.

In addition to the emergence of *T. bowmani*, nekton community change was driven by an increase in B/M species, largely composed of pelagic (*Anchoa mitchilli*, *Elops saurus*, *Brevoortia patronus*, Atherinopsidae) and benthic (*Citharichthys spilopterus*, Gobiidae) species. Most of the pelagic and benthic species that were captured in spring 2006 were not captured in spring 2007. This suggests that the period of elevated salinity following Katrina may have temporarily made upper basin marshes more favorable to B/M species and facilitated their

movement into upper estuary areas that are typically fresher. Species redistribution is common with changed physiochemical conditions (Paperno et al., 2006). The sudden influx of new species caused a decrease in species diversity due to a decrease in evenness (Magurran, 1988), a common pattern resulting from disturbance (Paperno et al., 2006; Switzer et al., 2006).

Our study also documented a shift in T/R fish species. Prior to Hurricane Katrina, T/R fishes were dominated by *H. formosa* and *Gambusia affinis*. However, in spring 2006, there was a pronounced decrease in these two species and an increase in *Lucania parva*. This shift in dominance was likely due to the elevated salinities following the storm, because these three species are functionally similar and inhabit similar habitats (Kneib 2000). While *H. formosa* and *G. affinis* have shown tolerance for high salinity in laboratory experiments, both species are typically found in fresher areas of the estuary (Nordlie and Mirandi 1996; Nordlie 2006). In contrast, *L. parva* exhibits a higher salt tolerance and is often found in higher salinity estuarine areas (Nordlie 2006). This shift in dominance is consistent with resilience theory, which suggests that after a disturbance there will be a dominance shift between functionally similar species with different tolerances for the stressor (Peterson et al., 1998).

### **Nekton Community Recovery and Ecosystem Resilience**

Nekton communities largely returned to pre-storm conditions (i.e. 2005) within 18 months of hurricane passage. These results agree with other studies in estuarine environments that show relatively short effects on biota and community structure and high ecosystem resiliency to hurricane pulses (Waide, 1991). These results are particularly interesting because the vegetation density and water level data from 2007 suggest that vegetated marsh habitat either was not recovering or was very slow to recover. Yet, despite the lack of vegetated marsh habitat, the nekton community returned to pre-storm conditions, an unexpected result because many estuarine resident and transient nekton species are critically dependent on the vegetated marsh



habitat. However, the effects of marsh loss are often not reflected in abundance of nekton, and this may be due to a temporary increase in marsh-edge habitat that occurs with marsh loss (Chesney et al. 2000).

This relatively quick return to pre-storm conditions may be due to the fact that the nekton community in our study was largely composed of generalist T/R species. In terrestrial systems that receive extreme physical damage, effects on biotic communities are often long-lasting. However, generalist species often remain largely unaffected. For example, in tropical forest ecosystems, insectivorous bird and bat species are often less affected and return to pre-hurricane levels relatively quickly as compared to canopy and frugivorous species (Waide, 1991). This same effect has been shown in bird and moth communities in response to forest clear cutting and other timber management strategies (Chambers et al., 1999; Pearson and Manuwal, 2001; Summerville and Crist, 2002).

This return to pre-storm conditions may also be due to mitigating effects of the Caernarvon freshwater diversion on salinity. The combination of the storm surge and extended drought conditions following passage of Hurricane Katrina resulted in a period of elevated salinities that persisted for approximately six months. This increase in salinity likely expanded the range of favorable habitat for B/M species to upper estuary marshes, while creating unfavorable conditions for T/R species with limited salt tolerance. However, once Caernarvon began discharging riverine water into the basin, prior to our sampling, salinity in upper Breton Sound quickly returned to pre-storm conditions, and salinity conditions were similar to pre-hurricane conditions through 2007. Therefore, the salinity effects from the storm did not persist, and our 2007 results show a consequential disappearance of B/M species and a return of T/R species that declined post-Katrina (*H. formosa*, *G. affinis*) to pre-storm levels.

It is also possible that this relatively rapid return to a pre-storm nekton community by spring 2007 may represent a sampling effect. Sample size during 2007 was very limited (N=9), due to equipment and logistical issues. Additionally, due to differences in timing of the freshwater pulses the sampling dates did not cover the same range of time as 2005 and 2006 samples. Perhaps the lack of B/M species (which were relatively rare) as well as the sharp decrease in *T. bowmani* in 2007 reflected this limited sampling effort. We know that sampling intensity affects species richness because the probability of capturing rare species increases with sample size (MacArthur and Wilson, 1967; Magurran, 1988). Small sample sizes often do not allow for an adequate spatial or temporal representation of the area being studied (MacArthur and Wilson 1967). Therefore, it is possible that our results may be biased toward common species in 2007. However, we tested this effect by randomly selecting nine samples from both 2005 and 2006 and comparing them against the 2007 samples. The resulting patterns for nekton abundance, diversity and community change were identical to those we found with the full data set. Therefore, we believe that this relatively rapid return to a pre-storm nekton community by spring 2007 was real and not a sampling effect.

### **CONCLUSION**

This study provides important and rare data regarding the effects of hurricane-induced disturbance on estuarine nekton communities in tidal freshwater areas that experienced extensive and enduring physical habitat effects. In particular, this study documents a certain amount of resilience by the estuarine nekton community in the face of enduring physical habitat change, and short-term chemical changes. Understanding the range of community change and resiliency that is experienced by a system in response to disturbance provides insight into ecosystem function and guide management and restoration of coastal systems.

## **LITERATURE CITED**

- Allen DA (1982) Autecology of the cryptic mysid crustacean, *Heteromysis formosa* S.I. Smith 1873, in a temperate estuary. *Hydrobiologia* 93:1-7
- Barras JA (2007) Satellite images and aerial photographs of the effects of Hurricanes Katrina and Rita on coastal Louisiana: U.S. Geological Survey Data Series 281, at <http://pubs.usgs.gov/ds/2007/281>
- Cahoon DR (2006) A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* 29:889-898
- Chambers CL, McComb WC, Tappeiner JC II (1999) Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. *Ecol Appl* 9:171-185
- Chesney EJ, Baltz DM, Thomas RG (2000) Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecol Appl* 10:350-366
- Day JW Jr, Boesch DF, Clairain EJ, Kemp GP, Laska SB, Mitsch, WJ, Orth K, Mashriqui H, Reed DJ, Shabman L, Simenstad CA, Streever BJ, Twilley RR, Watson CC, Wells JT, Whigham DF (2007) Restoration of the Mississippi Delta: lessons from Hurricanes Katrina and Rita. *Science* 315:1679-1684
- FEMA (2006) High water mark collection for Hurricane Katrina in Louisiana: Final Report. FEMA-1603-DR-LA, Task Orders 412 and 419. March 30, 2006
- Froese R, Pauly D, *Editors*. (2008) FishBase. World Wide Web electronic publication. [www.fishbase.org](http://www.fishbase.org), version (09/2008)
- Fritz HM, Blount C, Sokoloski R, Singleton J, Fuggle A, McAdoo BG, Moore A, Grass C, Tate B (2007) Hurricane Katrina storm surge distribution and field observations on the Mississippi barrier islands. *Est Coast Shelf Sci* 74:12-20
- Graumann A, Houston T, Lawrimore J, Levinson D, Lott N, McCown S, Stephens S, Wuertz D (2005) Hurricane Katrina: a climatological perspective. NOAA National Climatic Data Center. US Department of Commerce NOAA/NESDIS Technical Report 2005-01
- Greenwood MFD, Stevens PW, Matheson RE Jr (2006) Effects of the 2004 hurricanes on the fish assemblages in two proximate southwest Florida estuaries: change in the context of interannual variability. *Estuaries and Coasts* 29:985-996
- Hsu SA, Braud D, Blanchard B (2006) Rapid estimation of maximum storm surges induced by Hurricanes Katrina and Rita in 2005. *NWA Electronic J Operation Meteorol* 2006-EJ9
- Kneib RT (2000) Saltmarsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: M.P. Weinstein, D.A. Kreeger (Editors). *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Boston, MA, pp. 267-291

- Lane RR, Day JW Jr, Marx BD, Reyes E, Hyfield, E, Day JN (2007) The effects of riverine discharge on temperature, salinity, suspended sediment and chlorophyll a in a Mississippi delta estuary measured using a flow-through system. *Est Coast Shelf Sci* 74:145-154
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ. 203 pp
- Magurran AE (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ. 179 pp
- Nordlie FG, Mirandi A (1996) Salinity relationships in a freshwater population of eastern mosquitofish. *J Fish Biol* 49:1226-1232
- Nordlie FG (2008) Physicochemical environments and tolerances of cyprinodontoid fishes found in estuaries and salt marshes of eastern North America. *Rev Fish Biol Fish* 16:51-106
- Nyman JA, Crozier CR, Delaune RD (1995) Roles and patterns of hurricane sedimentation in an estuarine marsh landscape. *Est Coast Shelf Sci* 40:665-679
- Paperno R, Tremain DM, Adams DH, Sebastian AP, Sauer JT, Dutka-Gianelli J (2006) The disruption and recovery of fish communities in the Indian River Lagoon, Florida, following two hurricanes in 2004. *Estuaries and Coasts* 29:1004-1010
- Pearson SF, Manuwal DA (2001) Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-Fir forests. *Ecol Appl* 11:840-853
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18
- Piazza BP, La Peyre, MK (2007) Restoration of the annual flood pulse in Breton Sound, Louisiana, USA: habitat change and nekton community response. *Aquat Biol* 1:109-119
- Price WW (1982) Key to the shallow water Mysidacea of the Texas coast with notes on their ecology. *Hydrobiologia* 93:9-21
- Snedden GA, Cable JE, Swarzenski C, Swenson E (2007 A) Sediment discharge into a subsiding Louisiana deltaic estuary through a Mississippi River diversion. *Est Coast Shelf Sci* 71:181-193
- Snedden GA, Cable JE, Wiseman WJ (2007 B) Subtidal sea level variability in a Mississippi River deltaic estuary, Louisiana. *Estuaries and Coasts* 30:802-812
- Stevens PW, Blewett DA, Casey JP (2006) Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of Hurricane Charley. *Estuaries and Coasts* 29:997-1003
- Summerville KS, Crist TO (2002) Effects of timber harvest on forest Lepidoptera: community, guild, and species responses. *Ecol Appl* 12:820-835

- Switzer TS, Winner BL, Dunham NM, Whittington JA, Thomas M (2006) Influence of sequential hurricanes on nekton communities in a southeast Florida estuary: short-term effects in the context of historical variations in freshwater flow. *Estuaries and Coasts* 29:1011-1018
- Vilas C, Drake P, Fockedey N (2008) Feeding preferences of estuarine mysids *Neomysis integer* and *Rhopalophthalmus tartessicus* in a temperate estuary (Guadalquivir Estuary, SW Spain). *Est Coast Shelf Sci* 77:345-356
- Waide RB (1991) Summary of the response of animal populations to hurricanes in the Caribbean. *Biotropica* 23:508-512
- Yang LH, Bastow JL, Spence KO, Wright AN (2008) What can we learn from resource pulses? *Ecology* 89:621-634

## **CHAPTER 6**

### **SUMMARY AND CONCLUSIONS**

I examined the effect of climate variability on local estuarine nekton in Breton Sound, Louisiana within a framework that encompassed multiple spatial and temporal scales and attempted to link critical atmospheric processes with local community assembly filters that potentially affect estuarine nekton.

Chapter two identified a teleconnection between juvenile brown shrimp abundance in Breton Sound estuary and the El Niño Southern Oscillation (ENSO). ENSO affected winter weather conditions (air pressure, temperature and precipitation), and spring brown shrimp abundance in Breton Sound. Juvenile brown shrimp abundance effects lagged ENSO by three months; lower than average abundances of juvenile brown shrimp were caught in springs following winter El Niño events, and higher than average abundances of brown shrimp were caught in springs following La Niña winters. Salinity was the dominant ENSO-forced assembly filter for juvenile brown shrimp. Spring salinity was cumulatively forced by winter river discharge, winter wind forcing and spring precipitation. Although I did not investigate further the specific mechanisms through which climate affects shrimp populations, these results indicate that all years are not created equal and illuminate an important factor to consider when managing the fishery or restoring coastal wetland habitat.

Chapter three documented higher nekton density and biomass in marshes that received pulsed riverine flow than in marshes that did not receive pulsed flow. Differences in density and biomass were attributed to differences in water depth and flooding duration caused by the pulses. Communities were largely similar and consisted mainly of marsh resident species. An examination of individual species also revealed apparent habitat preferences related to water depth. These results suggest that pulsed riverine flow may enhance secondary productivity in

Breton Sound estuary, because increased nekton density, biomass and community assembly were directly attributed to factors associated with marsh surface flooding. The results provided the first step toward quantifying the potential energetic subsidy of riverine pulses to downstream habitats in the form of resident nekton.

Chapter four indicated that marshes flooded by pulsed riverine flow were capable of producing optimum growth ( $0.001 \text{ g DW d}^{-1}$ ) for an ubiquitous species, *G. affinis*. Additionally, these marshes contained  $> 6,000 \text{ cal g}^{-1}$  of resident nekton energy that was available for trophic transport to subtidal habitat. Additionally, analysis of experimental fish collected weekly through an extended pulse event showed two interesting growth-related pulses downstream from Caernarvon. The first was an immediate increase in energy density that occurred during weeks 1 – 3 of the pulse, and this pulse may be an indication of the immediate increase in food availability on the flooded marsh surface. A second growth pulse occurred during week five of the freshwater pulse and may represent either a delayed response to the increased food availability provided by the freshwater pulse or a secondary peak in prey items for *G. affinis*, such as invertebrates and mosquitoes.

Chapter five documented higher nekton densities and a shift from a nekton community consisting almost exclusively of Tidal freshwater / Resident (T/R) species toward one that included Brackish / Migrant (B/M) species after a direct hit by Hurricane Katrina in August 2005. Differences in nekton density were largely attributed to large catches of *Palaemonetes paludosus* and *Taphromysis bowmani*. *T. bowmani* is a mysid shrimp that was not captured in samples in the spring prior to the storm. The emergence of this species in drop samples, as well as the community shift toward B/M, especially those with pelagic and benthic life history strategies, was likely due to the combination of elevated salinity and the stark loss of vegetated marsh habitat that resulted from the hurricane winds and storm surge. Effects were short lived,

as by spring 2007, the nekton community had shifted back to T/R species, despite the lasting loss of vegetated marsh habitat. This result documents a certain amount of resilience by the estuarine nekton community in the face of enduring physical habitat change and short-term chemical changes caused by an extreme meteorological event. Understanding the range of community change and resiliency that is experienced by a system in response to climate-induced disturbance provides insight into ecosystem function and guide management and restoration of coastal systems.

Overall, this body of work provides evidence of large-scale climate effects on local estuarine nekton community dynamics and estuarine productivity. More research is needed into the specific mechanisms that operate to provide these controls. For example, Study one identified a teleconnection between winter ENSO conditions and spring brown shrimp abundance in Breton Sound estuary. Although this experiment identified the dominant assembly filter it did not investigate further the specific mechanisms through which climate affects shrimp populations. For example, the effects of salinity were not likely physiological but may have been an indirect trophic effect caused by lowered prey items in fresher conditions or, conversely, a preference for prey items in higher salinity areas. These types of interspecific mechanisms need to be studied further.

Next, the results indicate that all years are not created equal, and this illuminates an important factor to consider when managing the fishery or restoring coastal wetland habitat. Often, largescale freshwater releases through Caernarvon are perceived to be at odds with the brown shrimp fishery because of the possible effects on juvenile survival and growth in the estuary. While these factors are critical to the year-class strength of the fishery resource, the data identified a trend toward lower abundance following El Nino and higher abundance following La Nina. This information can assist managers to develop forward-looking strategies that balance



the need for fresh water with the needs of the fishery by maximizing potential benefits to each when conditions are conducive. For example, it may not be advantageous to manage for ‘average’ conditions every year, but rather a boom-and-bust method where large freshwater releases are maximized during El Niño events when shrimp abundance is low and vice versa. This example shows one way these types of studies can be used for adaptive management, especially as future pressure on estuarine systems increases.

Additionally, I found that riverine pulses resulted in higher nekton abundance and biomass, as well as higher fish growth. While this research shows a net benefit from flooding, it does not address, what I consider to be the most important next step which is “How much is too much.” If we consider the Pulsing Paradigm, in regards to not only my work, but all the work that has been done at Caernarvon, we can surmise that we are under this curve somewhere. The question is where, and when do these pulses become abrasive press disturbances. This question has important ramifications with regard to climate, because future climate predictions show that certain estuaries will receive significant increases in discharge – resulting in both greater pulse and press disturbance to habitats. This question has important ramifications to management and restoration because freshwater diversions are an important component of the Louisiana coastal restoration program, yet we do not fully understand how to manage them to optimize system benefits. For example, in an attempt to wring out all the sediment possible in response to land loss, we may be crossing a productivity threshold where pressed flooding decreases system benefits, yet there is extremely limited scientific data on this critical issue. Therefore, we need study of the effects of current diversion management, especially with respect to the duration of both high and low flow. We would be well served in investigating this important question, because freshwater management is only going to become more important moving forward.

Lastly, I found a certain amount of resilience by the tidal freshwater nekton community after a direct strike by Hurricane Katrina, in the face of enduring physical habitat change, and short-term chemical changes. Understanding this change and resiliency in response to disturbance provides insight into ecosystem function and can help guide management and restoration of coastal systems. Additionally, because one can never design for a hurricane strike, this type of study shows the importance of long-term studies and monitoring of coastal resources to expand our knowledge of ecological systems.

It is important to note that this dissertation is not meant to be a treatise on climate change; nor is its purpose to assess whether climate variability is good or bad. Rather it is meant to take one step toward a better understanding of the linkage between climate and estuaries and to illuminate additional research questions that need even better answers. If this work has accomplished these two things, then it has been a success.

## APPENDIX A

### CHAPTER 2 SUPPLEMENTAL GRAPHS

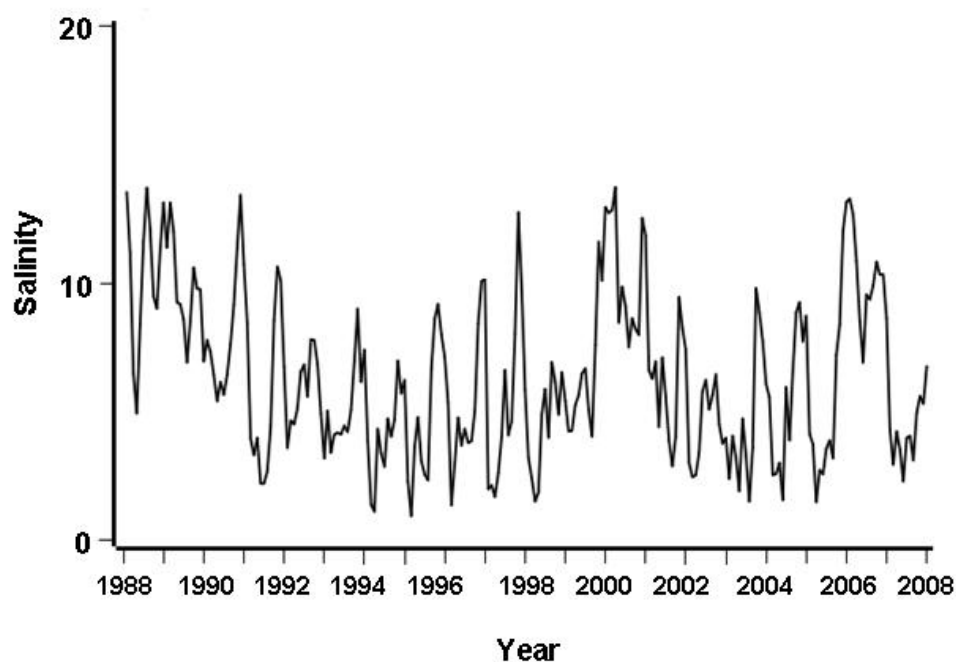


Fig. A.1. Graph of salinity in Breton Sound estuary, Louisiana from 1988 – 2007. Time series is based on monthly means of discrete samples pooled across stations 244, 255, 250, and 251.

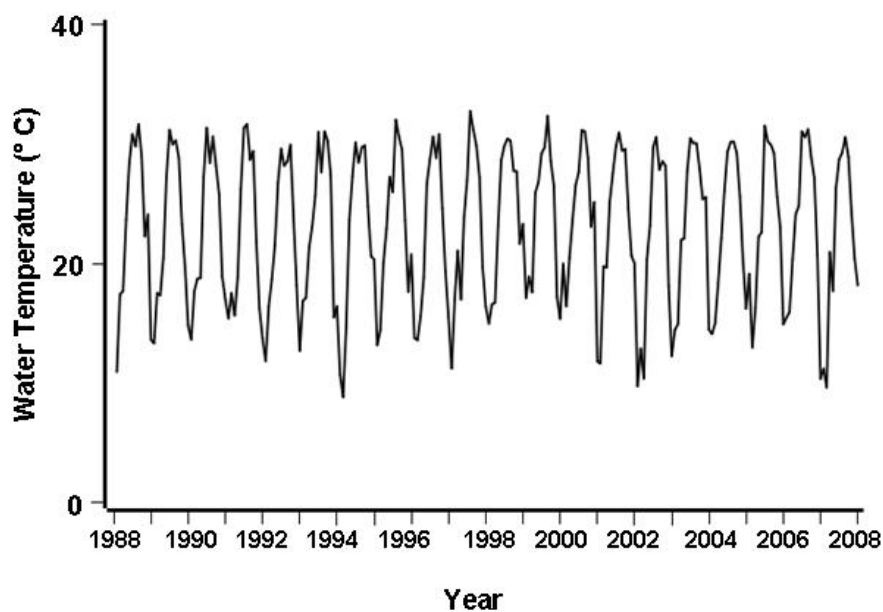


Fig. A.2. Graph of water temperature (° C) in Breton Sound estuary, Louisiana from 1988 – 2007. Time series is based on monthly means of discrete samples pooled across stations 244, 255, 250, and 251.

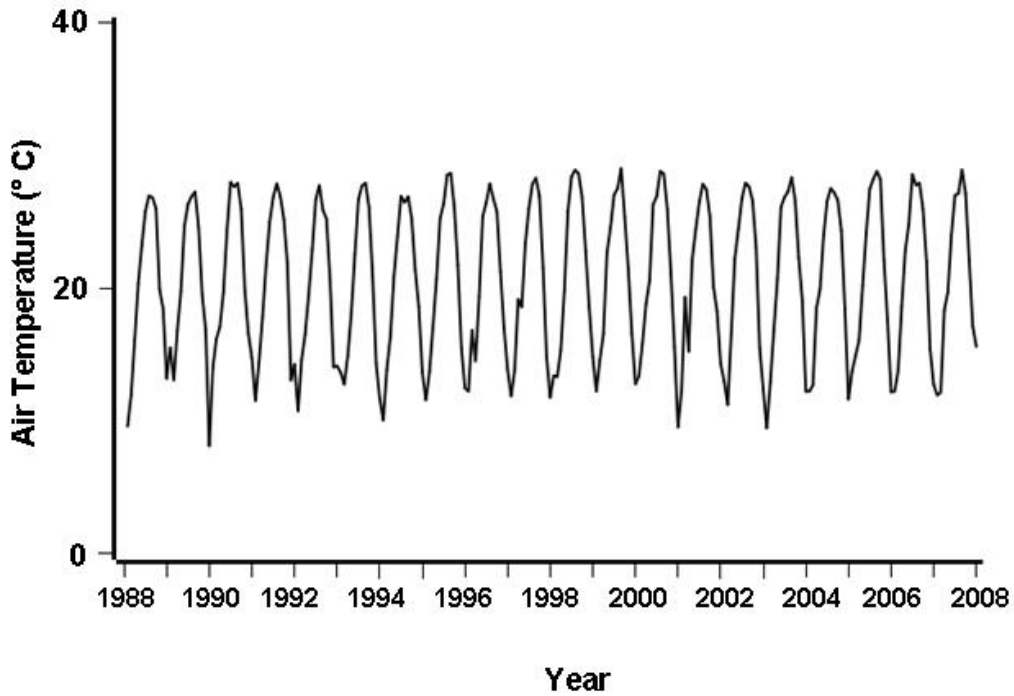


Fig. A.3. Graph of air temperature ( $^{\circ}$  C) taken at the New Orleans International Airport (Sta. Id. 166295) from 1988 – 2007. Time series is based on monthly means of continuous hourly readings.

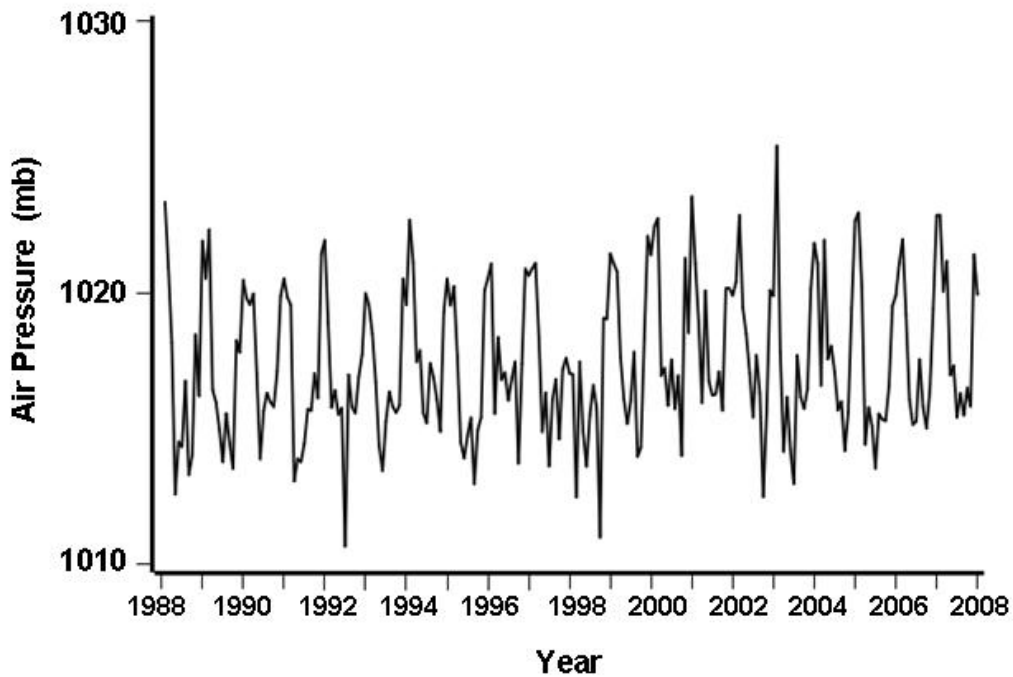


Fig. A.4. Graph of air pressure (mb) taken at the New Orleans International Airport (Sta. Id. 166295) from 1988 – 2007. Time series is based on monthly means of continuous hourly readings.

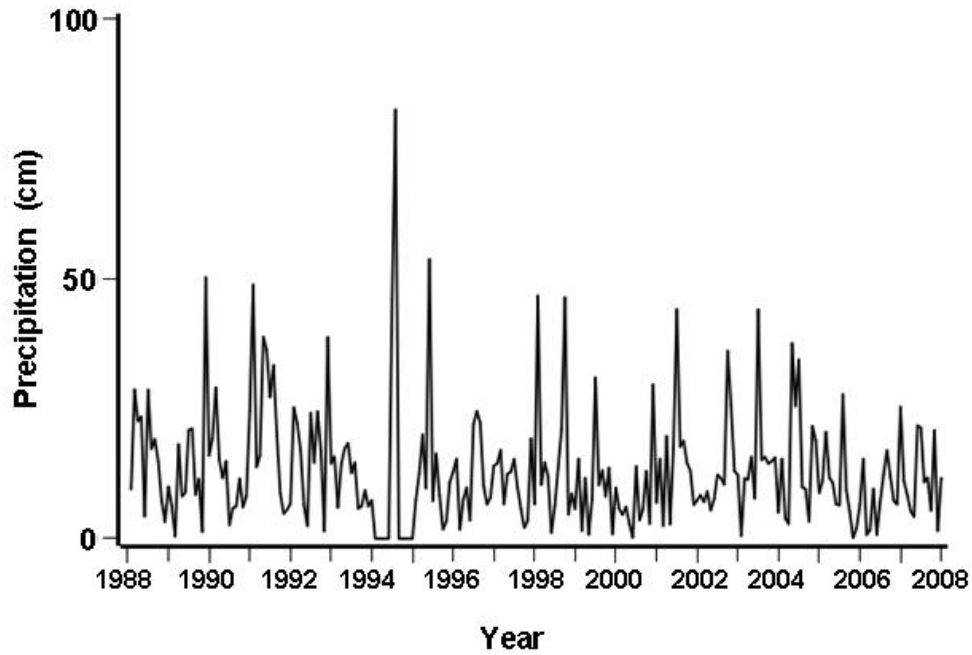


Fig. A.5. Graph of precipitation (cm) taken at the New Orleans International Airport (Sta. Id. 166295) from 1988 – 2007. Time series is based on monthly means of continuous hourly readings.

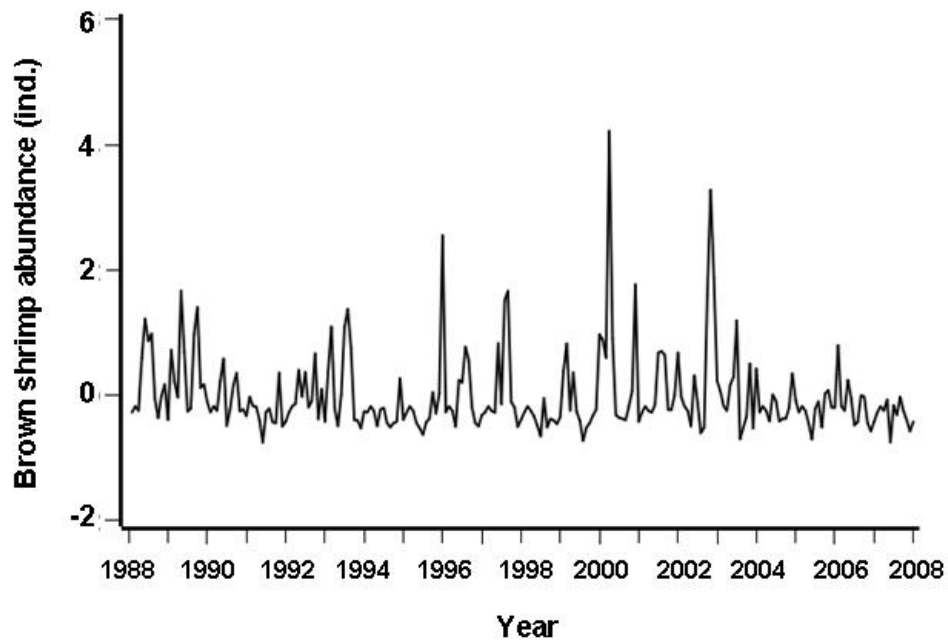


Fig. A.6. Graph of normalized juvenile brown shrimp abundance in Breton Sound estuary, Louisiana from 1988 – 2007. Time series is based on monthly means of discrete seine samples normalized by the mean and standard deviation and pooled across stations 244, 255, 250, and 251.

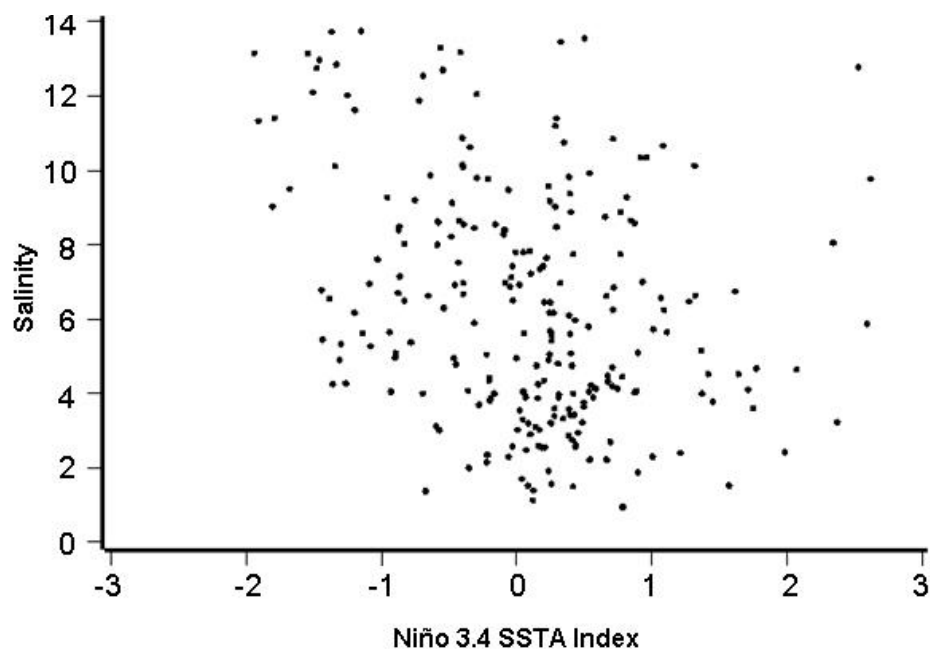


Fig. A.7. Graph of the monthly Nino 3.4 SSTA index and monthly salinity in Breton Sound estuary, Louisiana. Graph is based on the six-month running mean of the Nino 3.4 SSTA and monthly mean salinity from discrete samples pooled across stations 244, 255, 250, and 251.

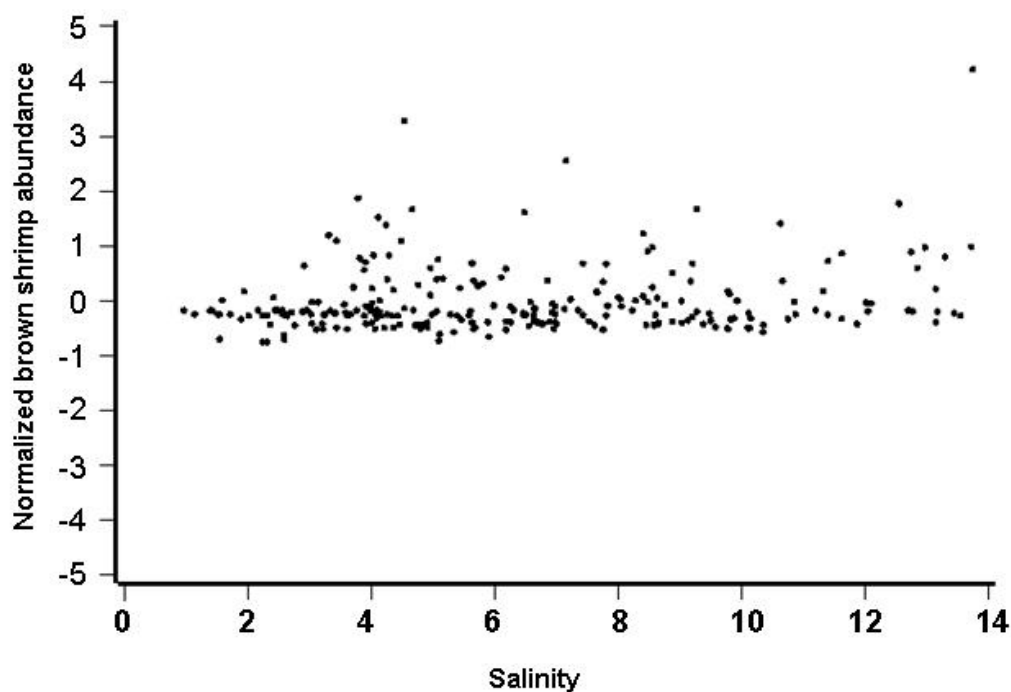


Fig. A.8. Graph of the monthly salinity and juvenile brown shrimp abundance in Breton Sound estuary, Louisiana. Salinity values are monthly means pooled across stations 244, 255, 250, and 251. Brown shrimp abundance values are monthly means of normalized values (normalized by the mean and standard deviation) pooled across stations 244, 255, 250, and 251.

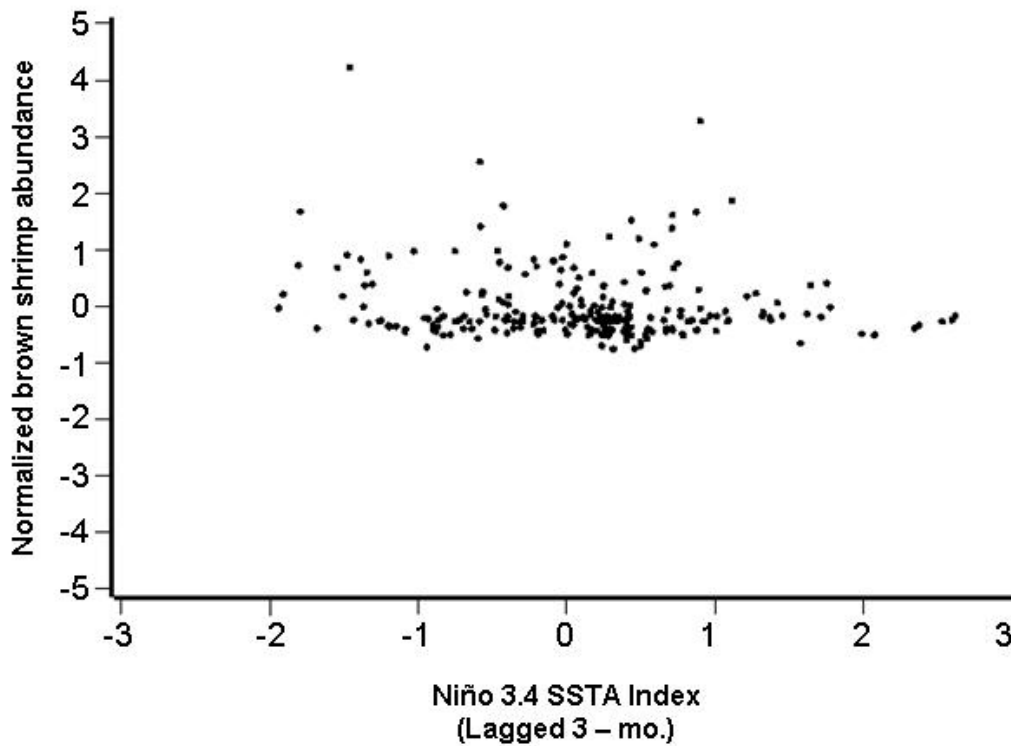


Fig. A.9. Graph of the monthly state of the ENSO and monthly juvenile brown shrimp abundance in Breton Sound estuary, Louisiana. ENSO values are the six-month running mean of the Niño 3.4 SSTA index. Brown shrimp abundance values are monthly means of normalized values (normalized by the mean and standard deviation) pooled across stations 244, 255, 250, and 251.

## APPENDIX B

### LETTER REQUESTING REPRINT PERMISSION



#### SCHOOL OF RENEWABLE NATURAL RESOURCES

227 Renewable Natural Resources Bldg. – LSU

Baton Rouge, Louisiana 70803-6202

(225) 578-4131

Fax: (225) 578-4227

Web site: [www.rnr.lsu.edu](http://www.rnr.lsu.edu)

[www.lsuagcenter.com](http://www.lsuagcenter.com)

January 13, 2009

Dr. Otto Kinne  
Editor-in-Chief  
Aquatic Biology  
International Ecology Institute  
Nordbunte 23  
21385 Oldendorf/Luhe  
Germany  
[kinne@int-res.com](mailto:kinne@int-res.com)

Dr. Kinne:

The purpose of this letter is to request permission to include the published paper by Bryan P. Piazza and Megan K. La Peyre titled "Restoration of the annual flood pulse in Breton Sound, Louisiana, USA: habitat change and nekton community response" as a chapter of my Ph.D. dissertation at Louisiana State University. This paper was published in *Aquatic Biology* 1: 109-119, 2007.

Sincerely,

A handwritten signature in black ink, appearing to read "Bryan P. Piazza". The signature is stylized with a large, looping "P" and a long horizontal stroke extending to the left.

Bryan P. Piazza  
School of Renewable Natural Resources  
Louisiana State University Agricultural Center  
Baton Rouge, LA 70803  
225-578-4199 tel.  
225-578-4144 fax  
[bpiazza@lsu.edu](mailto:bpiazza@lsu.edu)





# Inter-Research Science Center

Nordbunte 23 (+5/21/3  
21385 Oldendorf/Luhe  
Germany  
Tel +49 4132 7127  
Fax +49 4132 8883  
email [ir@int-res.com](mailto:ir@int-res.com)  
Internet [www.int-res.com](http://www.int-res.com)

Dr. Bryan P. Piazza  
School of Renewable Natural Resources  
Louisiana State University Agricultural Center  
Baton Rouge, LA 70803  
USA

14 January 2009

Dear Dr. Piazza,

We herewith give publisher permission for you to reprint the below mentioned paper, provided proper acknowledgement is being made to the original source of publication.

**Article:**

Restoration of the annual flood pulse in Breton Sound, Louisiana, USA: habitat change and nekton community response

**Authors:**

Bryan P. Piazza and Megan K. La Peyre

**Publication:**

Aquatic Biology 1: 109-119, 2007.

Sincerely,

Professor Dr. Dr. h. c. Otto Kinne  
-President Inter-Research Science Center-

**President**  
**Prof. Dr. Dr. h.c. Otto Kinne**

**JOURNALS**

Marine Ecology  
Progress Series  
Aquatic Biology

Aquatic  
Microbial  
Ecology

Climate  
Research

Diseases  
of Aquatic  
Organisms

Ethics in  
Science and  
Environmental  
Politics

Endangered  
Species  
Research

**BOOK SERIES**

Excellence  
in Ecology  
Top Books

**DISCUSSION  
FORUMS**

**RESEARCH**

Endangered  
Species  
Programs

**INSTITUTIONS**

International  
Ecology  
Institute

Eco-Ethics  
International  
Union

**FOUNDATION**

Otto Kinne  
Foundation

**Administration**  
(Verwaltung)



**SCHOOL OF RENEWABLE NATURAL RESOURCES**

227 Renewable Natural Resources Bldg. – LSU

Baton Rouge, Louisiana 70803-6202

(225) 578-4131

Fax: (225) 578-4227

Web site: [www.rnr.lsu.edu](http://www.rnr.lsu.edu)

[www.lsuagcenter.com](http://www.lsuagcenter.com)

March 20, 2009

Dr. Eric Wolanski  
Editor  
Estuarine, Coastal and Shelf Science  
[e.wolanski@aims.gov.au](mailto:e.wolanski@aims.gov.au)

Dr. Wolanski:

The purpose of this letter is to request permission to include the accepted paper by Bryan P. Piazza and Megan K. La Peyre titled "The effect of Hurricane Katrina on nekton communities in the tidal freshwater marshes of Breton Sound Louisiana, USA" (ECSS-D-09-00043R1) as a chapter of my Ph.D. dissertation at Louisiana State University. This paper was accepted for publication in Estuarine, Coastal and Shelf Science and has been forwarded it to the Journal Manager at Elsevier Production Department.

Sincerely,

A handwritten signature in black ink, appearing to be "B. Piazza", written over a horizontal line.

Bryan P. Piazza  
School of Renewable Natural Resources  
Louisiana State University Agricultural Center  
Baton Rouge, LA 70803  
225-578-4199 tel.  
225-578-4144 fax  
[bpiazza@lsu.edu](mailto:bpiazza@lsu.edu)



<http://www.elsevier.com>

## COPYRIGHT

### What rights do I retain as a journal author\*?

### When Elsevier changes its journal usage policies, are those changes also retroactive?

### How do I obtain a Journal Publishing Agreement?

### Can I post my article on the Internet?

### Why does Elsevier request transfer of copyright?

### Why does Elsevier believe it needs exclusive rights?

### Can you provide me with a PDF file of my article?

### What is Elsevier's policy on plagiarism and conflicts of interest?

### What rights do I retain as a journal author\*?

As a journal author, you retain rights for large number of author uses, including use by your employing institute or company. These rights are retained and permitted without the need to obtain specific permission from Elsevier. These include:

- the right to make copies (print or electric) of the journal article for their own personal use, including for their own classroom teaching use;
- the right to make copies and distribute copies (including via e-mail) of the journal article to research colleagues, for personal use by such colleagues (but not for Commercial Purposes\*\*, as listed below);
- the right to post a pre-print version of the journal article on Internet web sites including electronic pre-print servers, and to retain indefinitely such version on such servers or sites (see also our information on [electronic preprints](#) for a more detailed discussion on these points);
- the right to post a revised personal version of the text of the final journal article (to reflect changes made in the peer review process) on the author's personal or institutional web site or server, incorporating the complete citation and with a link to the Digital Object Identifier (DOI) of the article;
- the right to present the journal article at a meeting or conference and to distribute copies of such paper or article to the delegates attending the meeting;
- for the author's employer, if the journal article is a 'work for hire', made within the scope of the author's employment, the right to use all or part of the information in (any version of) the journal article for other intra-company use (e.g. training), including by posting the article on secure, internal corporate intranets;
- patent and trademark rights and rights to any process or procedure described in the journal article;
- **the right to include the journal article, in full or in part, in a thesis or dissertation;**
- the right to use the journal article or any part thereof in a printed compilation of works of the author, such as collected writings or lecture notes (subsequent to publication of the article in the journal); and
- the right to prepare other derivative works, to extend the journal article into book-length form, or to otherwise re-use portions or excerpts in other works, with full acknowledgement of its original publication in the journal.

**\*Please Note:** The rights listed above apply to journal authors only. For information regarding book author rights, please contact the **Global Rights Department**.

Elsevier Global Rights Department  
phone (+44) 1865 843 830  
fax (+44) 1865 853 333  
email: [permissions@elsevier.com](mailto:permissions@elsevier.com)

Other uses by authors should be authorized by Elsevier through the **Global Rights Department**, and journal authors are encouraged to let Elsevier know of any particular

- [Obtain permission to use Elsevier material](#)

Your question not found here?

- [Submit question](#)
- [Specific contacts](#)

## VITA

Bryan Patrick Piazza was born in November 1970, in Milwaukee, Wisconsin. He is the son of Patricia and Ronald Piazza and the younger brother of Bradley Piazza. He graduated from Thomas More High School in 1988. Bryan attended the University of Wisconsin – Stevens Point and graduated in 1993 with majors in wildlife management and biology and minors in natural resource management and environmental communications.

In 1993, Bryan entered the graduate program in wildlife ecology at LSU. He studied the nesting dynamics on wading bird rookeries in the Atchafalaya Delta, Louisiana. Bryan graduated with a Master of Science degree in 1997, while working as a wildlife manager at Guana River Wildlife Management Area, in Ponte Vedra Beach, Florida (Florida Fish and Wildlife Conservation Commission). After a short time in Florida, Bryan returned to Baton Rouge to work in policy development and restoration planning for the Louisiana Department of Natural Resources, Coastal Restoration Division.

In 2002, Bryan accepted a position as a research associate in Megan La Peyre's lab in the School of Renewable Natural Resources, at LSU. Since that time he has performed wetland ecology and fisheries research in marshes across the coast. He entered the doctoral program in the Department of Oceanography and Coastal Sciences as a part-time student in August 2004 and will graduate in May 2009. Bryan has accepted a position with The Nature Conservancy of Louisiana, where he will direct science, conservation, and restoration for the Atchafalaya River Basin and Bays Program. He is married to Sarai and has a newborn baby, Kade.